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Effects of overstory tree species and seed trap design on seed rain in a tropical rainforest

Bridgette Kirk
Iowa State University

Effects of overstory tree species and seed trap design on seed rain in a tropical rainforest

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Bridgette Kirk

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Brian Wilsey, Co-major Professor
Haldre Rodgers

The student author, whose presentation of the scholarship herein was approved by the program of study committee, is solely responsible for the content of this thesis. The Graduate College will ensure this thesis is globally accessible and will not permit alterations after a degree is conferred.

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ABSTRACT

Tropical rainforests maintain a high diversity of plant species, but the community assembly mechanisms by which this occurs are unclear. We hypothesized that individual overstory tree species could filter seed rain differentially, owing to differences in species-specific traits that affect forest physiognomy and resources for animals, which in turn influence likelihood of arrival of wind- and animal-dispersed seeds. Quantifying the effects of an individual tree species on seed rain in a highly diverse natural forest is challenging, and thus understudied. Seed rain of very small seeds (<1 mm long) is also relatively uncharacterized because seed trap mesh size is usually ≥1 mm. In a unique experimental setting containing replicated, monodominant, 26-yr-old plantations of four native tree species at La Selva Biological Station (Costa Rica), we studied the effects of four native tree species on seed rain. We collected seed rain of woody species for 14 months in 15 50-×-50-m plots from 75 traps. In each plot three traps were lined with Terylene® fabric of 1-µm (fine) mesh and two with 1-mm (regular) mesh.

Across all traps, the total annual seed rain was 133,355 seeds from 121 woody species representing 41 families. Seed rain differed significantly among the four overstory tree species with respect to species richness and composition. Species richness was lowest in *Pentaclethra macroloba*, the only species in our experiment that was not animal-dispersed or predated. Total abundance, species richness, diversity and composition of seed rain varied significantly between fine- and regular-mesh traps. Regular-mesh traps underestimated species richness by 50% and missed 90% of the very-small-seeded species in seed rain. This indicated that the seed trap mesh size could significantly affect interpretations about life form and successional proclivity of species arriving in seed rain, with consequences for evaluation

of restoration strategies. These results suggest that individual tree species influence potential disperser behavior, and therefore seed dispersal patterns, by virtue of differences in food resources provided by tree species. Individual tree species can filter seed dispersal, thereby influencing its own local neighborhood at the onset of plant community assembly, seed arrival.

CHAPTER 1. INTRODUCTION

Background

Tropical rainforests have high plant diversity which is thought to be maintained by limited seed dispersal. While temperate ecoregions may have between 500-1000 plant species, tropical rainforests contain over 5,000 plant species (Kier et al. 2005). Costa Rica is considered the global biodiversity hotspot for vascular plants (Barthlott et al. 2007). Thus, tropical rainforests provide ideal systems to understand processes underlying the maintenance of such high diversity (Wright 2002). One such community assembly process is seed dispersal, which shapes the spatial distribution and variation of species in seed rain (HilleRisLambers et al. 2012, Beckman and Rogers 2013, Vellend 2016). The seed rain contains species available for regenerating seedlings, established saplings and ultimately reproducing adults.

In tropical rainforests over 80% of tree and shrub species are animal dispersed and therefore, disperser preferences and behavior play a role in plant species distributions (Howe and Smallwood 1982, Wunderle 1997, Clark et al. 2004). Many studies have found that contagious seed dispersal or clumped distributions with high density-dependent mortality results from the higher fraction of species with animal-dispersed seeds (Clark et al. 2004). Conversely, wind-dispersed species are often presumed to be randomly distributed through the landscape and are based on wind patterns (Kuparinen 2006). Thus, traits of species in seed rain can be explored as mechanisms that affect species distributions.

Functional traits of overstory tree species including tree physiognomy and resources provided to dispersers have the potential to influence local species composition as a result of their functional traits. Fruiting trees act as recruitment foci by attracting potential dispersers

to a specific neighborhood (Slocum 2001, Trolliet et al. 2017). The propagule type (dry, fleshy, etc.) of tree species is a functional trait that can affect attractiveness to dispersers thereby changing spatial variation in seed rain. Additionally, the physiognomy of overstory tree species can affect airflow and wind velocities, thus changing the trajectory of wind-dispersed seeds.

Most seed rain studies in the tropics utilize mesh-lined traps with mesh sizes ranges from 0.13 mm to 2 mm, with the most commonly used size being 1 mm (de Melo et al. 2006, Zamora and Montagnini 2007, Blackham et al. 2013, Wright et al. 2016, Rose et al. 2017). Given that for some species, seeds are smaller than 1 mm, it is possible that species are not being captured in these traps (Hardesty and Parker 2003). In particular, early successional species and wind-dispersed species tend to have small seeds. If these seed traps captured fewer species in seeds of those two functional groups, it could impact the inferences made about succession and dispersal modes. For restoration projects, this would affect conclusions about seed limitation and successional trajectory.

Current research has not quantified which species are potentially missed by using a mesh size not designed to capture seeds of all species. Additionally, we are not aware of any study that has attempted to isolate the effects of a single tree species in the context of a highly diverse rainforest. Previous studies have found that overstory tree species can alter composition and diversity of understory woody regeneration; however, the species-specific traits which are responsible for these differences remain unconfirmed (Powers et al. 1997, Guarigata and Ostertag 2001, Zamora and Montagnini 2007).

Questions and Objectives

The main objectives of this research were to examine whether overstory tree species differentially affected species arrival in seed rain and determine whether mesh size in seed

traps resulted in different seed rain composition. In Chapter 2, we quantified the effect of overstory tree species on seed rain and analyzed how overstory species influenced seed dispersal filtering by comparing functional traits of species in seed rain and those of the overstory tree species. We specifically analyzed for differences in total abundance, species richness, diversity and composition in the seed rain. In Chapter 3, we examined differences in seed rain between two sizes of mesh in seed traps to quantify and characterize the effect of mesh size on species capture and evaluate the consequences for interpretations. We also considered the importance of capturing all available species for evaluating restoration strategies.

Experimental Setting

This research was conducted in the Costa Rican Atlantic lowlands at La Selva Biological Station. This 1500-ha forest is surrounded by agricultural plantations, pastures for cattle grazing and Braulio Carrillo National Park. The randomized complete block design for this experiment, initiated in 1988, originally contained 11 treatments and one control in four blocks (Fisher 1995). Each block was topographically centered around a hill with tree species assigned in a stratified random manner, such that each species occurred in each topographic position (hilltop, slope, and bottom of hill) across the four blocks (Fisher 1995). The treatment consisted of a single overstory tree species planted in a 50-×-50-m plot. Trees were planted at a spacing of 3 × 3 m with some understory thinning until 3-4 years (Haggar et al. 1997, Powers et al. 1997). Within each plot, a subplot treatment of mesh sizes was applied randomly to the five seed traps. Seed traps were initially placed within the plots on 13 January 2014 by the field crew and then checked approximately weekly for 14 months. Three traps per plot were lined with a fine-mesh Terylene® fabric (1 µm) and the remaining two traps contained 1 mm mesh. By 2014, 26 years after establishment of experiment, only four

native overstory tree species were alive in all four blocks: *Hieronyma alchorneoides* Allemão, *Pentaclethra macroloba* (Willd.) Kunth., *Virola koschnyi* Warb., and *Vochysia guatemalensis* Donn. Sm. Our study site can uniquely disentangle the effects of a single overstory tree species because other factors are similar across the experimental overstory tree species.

Thesis Organization

Chapter 1 is a general introduction to the study system and current research related the field of seed dispersal ecology in tropical rainforests. Chapter 2 is an article written to be submitted to the journal *Ecology*. In this chapter, I assessed the effects of overstory tree species on the composition and diversity of seed rain. I also characterized the four experimental overstory tree species and evaluated their relationships with observed differences in seed rain. Chapter 3 is an article to be submitted to the journal *Methods in Ecology and Evolution*. In this chapter, I evaluated two mesh sizes used in seed rain traps in tropical rainforests. We specifically evaluated differences in species composition and richness between the two mesh sizes and discussed implications of mesh size in seed traps. Chapter 4 includes a general conclusion to this research, future directions of study and concluding remarks. The results from this thesis provide insights into seed dispersal processes that influence diversity in tropical rainforests, insight of mesh size in seed traps on analysis and interpretation of results for testing hypotheses, and implications for tropical rainforest restoration.

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CHAPTER 2. TREE SPECIES DIFFER IN THEIR FILTERING EFFECT ON SEED RAIN IN A TROPICAL RAINFOREST

Modified from a paper to be submitted to *Ecology*

Bridgette D. Kirk[1,2], Ann. E. Russell[1], Sabrina Russo[3], Haldre S. Rogers[4], Orlando Vargas[5], Ricardo Bedoya[6]

Abstract

Tropical rainforests contain high plant species diversity, which can be maintained through mechanisms that limit seed dispersal, and thus cause spatial variation in the species composition of the seed rain. We posited that individual overstory tree species mediate seed rain because of differences in traits such as tree physiognomy and resources for animals, thereby influencing seed rain of wind- and animal-dispersed species. We predicted that overstory tree species with traits that attract dispersers through resources provided by or structure of the tree species will increase the abundance and diversity of species arriving as seeds. The influence of overstory tree species on the diversity and abundance of seeds arriving in the seed rain are relatively understudied, however, given the challenge of isolating the effect of an individual species in highly diverse natural forests. In an experiment containing 26-yr-old, monodominant, plantations replicated across four native overstory tree species, two animal-dispersed and two abiotically dispersed species, across four blocks at La Selva Biological Station (Costa Rica). We studied the effects of the identity and traits of overstory tree species on seed arrival. We collected seed rain of woody species monthly for

[1] Department of Natural Resource Ecology and Management, Iowa State University, Ames, Iowa 50011 USA
[2] Primary researcher and author for correspondence
[3] School of Biological Sciences, University of Nebraska, Lincoln, Nebraska 68588 USA
[4] Department of Ecology, Evolution and Organismal Biology, Iowa State University, Ames, Iowa 50011 USA
[5] Organization for Tropical Studies, Puerto Viejo de Sarapiquí, Costa Rica
[6] Fondo Nacional de Financiamiento Forestal, Costa Rica

14 months to evaluate: 1) whether seed rain differed in overall abundance, species richness, diversity and composition among overstory tree species plantations; and 2) how variation in seed rain related to traits of the overstory tree species and traits of seed-rain species including dispersal mode, life form, seed size, and successional status. Although abundance and Shannon-Weiner diversity of the seed rain did not differ among overstory tree species, species richness and composition did. *Pentaclethra macroloba* plots contained fewer animal-dispersed species arriving as seeds than the three other overstory tree species, which may be attributed to the lack of food resources for potential animal dispersers. The significant correlations between traits of the seed rain and the overstory species suggests that overstory species influence seed rain, potentially due to differences in resources provided for animal-dispersed species. These results indicate that individual overstory tree species affect initial neighborhood community assembly through seed-dispersal filtering which will influence later stages of plant regeneration.

Introduction

Continental tropical rainforests maintain the highest plant species diversity globally yet the underlying community assembly mechanisms responsible are not well known. Tropical rainforest diversity can exceed 5,000 plant species, approximately five times that of temperate ecoregions (Kier et al. 2005). Therefore, tropical rainforests provide unique settings to evaluate processes that maintain species diversity. Seed dispersal is one such process that influences community assembly by spatially and temporally filtering the distribution and composition of seed rain (Vellend 2010, Götzenberger et al. 2012, HilleRisLambers et al. 2012, Beckman and Rogers 2013, Traveset et al. 2014). Seed dispersal is often assumed to be global, random or historically contingent on past disturbance

events and land uses (Chase 2003, Fukami et al. 2005, Paine and Harms 2009, Fukami 2010, Vellend 2016). However, theory suggests that regional diversity is maximized when dispersal is limited (Caswell and Cohen 1991). In other studies however, dispersal was found to be deterministic, or caused by interactions between species and their environments. These differing results highlight the need for a better understanding of the mechanisms underlying dispersal (Chapman et al. 2016) and their relationships with maintenance of species diversity.

The mechanisms by which seeds are dispersed, including wind, animal, water, ballistic or gravity, influence the potential area reached by seeds, and thus the likelihood of seed arrival (Levin et al. 2003, Beckman and Rogers 2013). Vegetation density can affect wind patterns and collision rates that influence dispersal distances for wind-dispersed species (Pounden et al. 2008). Although seed rain was limited at the start of gap regeneration, wind-dispersed species were more common in seed rain owing to higher overall dispersal success and dispersal distances from the parent crown relative to seeds of animal-dispersed species (Puerta-Piñero et al. 2013). This non-random dispersal of wind-dispersed seeds can alter the pool of species available for regeneration. Animal dispersal adds variation to seed distributions, given coupled interactions between the disperser and the plant being dispersed (Stoner 1996, Russo et al. 2006, Puerta-Piñero et al. 2013, Simmons et al. 2018). In temperate forests, 10-25% of trees and 85-100% of shrubs and woody vines are animal-dispersed (Howe and Smallwood 1982). In contrast in tropical rainforests, over 80% of woody species are animal dispersed and thus heavily influenced by their dispersers (Howe and Smallwood 1982). As a result, animal dispersal is deterministic, owing to traits of the disperser (Lowe and McPeek 2014, Chapman et al. 2016). Thus, most studies of seed dispersal have focused on the disperser or traits of the species being dispersed.

Overstory trees have the potential to differ in their effects on filtering seed rain, owing to differences in species-specific traits that result in differential provisioning of resources for animal-dispersers and differences in wind patterns. Tree species with fleshy propagules or fruit attract animal dispersers to the individual tree that may then disperse seeds of other species' in the process; the attractiveness of the tree's fruit is correlated with seed rain beneath it (McDonnell and Stiles 1983, Loiselle 1990, Wunderle 1997, Clark et al. 2004, Sansevero et al. 2011, Trolliet et al. 2017). The relative attractiveness of the fruit may depend on the specific disperser, and thus limits arrival of woody species in seed rain to species preferentially fed on by the attracted dispersers (Slocum 2001). Additionally, trees provide structure for roosting, resting, and nesting for bats and birds (Kelm et al. 2008); differences among tree species in their structure could thus result in differential seed rain. Variation in structural traits may also lead to differences in microclimates, thus differentially imposing an additional filter for the disperser (Hirai et al. 2014). Tree physiognomy also affects wind velocity and direction, thus differences among tree species can influence distance travelled by wind-dispersed seeds (Bohrer et al. 2008).

We focus in this study on the effect of the overstory tree species to which seed rain arrives, at the level of a single overstory tree species. Locally patchy seed rain may exist because tree species differ in traits that could influence both wind patterns and behavior of animals that disperse seeds. Because seed arrival establishes the initial template of species available for regeneration, local filtering of seed rain by overstory tree species could affect spatial variation in regeneration, and ultimately, forest community assembly. Understanding the extent to which overstory tree species differ in their effects on seed rain is particularly important in secondary forests, as it has implications for restoration and development of

effective management strategies. Under typical conditions in an old-growth tropical rainforest, the effects of a single tree species are difficult to disentangle from other factors affecting spatial variation in seed rain. We used experimental plantations consisting of monodominant stands of four native tree species to test whether overstory tree species differed in their effects on local filtering of the seed rain.

The objectives of this study were to evaluate whether individual overstory tree species differ in their influence on seed rain and to evaluate functional species traits that may affect seed dispersal. We compared annual seed rain across four replicated, monodominant, plantations of four native overstory trees, two animal-dispersed species and two abiotically dispersed species, with these specific research goals: (1) to quantify the effect of the individual tree species on seed rain and, (2) to evaluate correlations between traits of the seed-rain species and the overstory tree species. We hypothesized that abundance and diversity of seed rain would be higher in the animal-dispersed overstory tree species, the rationale being that more potential dispersers are attracted to those plots. We also posited that abundance and diversity of seed rain would be correlated with overstory tree species whose physiognomy was attractive to animal dispersers and that differences in the tree species traits could influence wind-dispersed seed arrival. Considering the age of these plots, we predicted fewer species would be arriving as seeds that were not already present within the plots. We interpret our results in light of their consequences for forest community assembly, both in terms of mechanisms for maintaining species diversity in old-growth forests, and regeneration and restoration in disturbed and fragmented tropical secondary forests.

Methods

Study Site

This study was conducted in the Atlantic lowlands of Costa Rica at La Selva Biological Station (hereafter, "La Selva") (10° 26' N, 84° 01' W). The surrounding landscape includes agricultural pastures, plantations, small farms to the north (Butterfield 1994) and old-growth forest upslope in Braulio Carrillo National Park. The specific experimental site is bordered on the north and west by the Peje River, on the east by abandoned pastures and on the south by old-growth forest within La Selva (Butterfield 1994). Mean annual rainfall is 4000 mm and mean annual temperature is 25.8°C with no distinct dry season (Sanford et al. 1994), although February through April are drier months. The topography is hilly, with mean elevation ranging from 40 to 100 m above mean sea level (Haggar et al. 1997). Historical contingency based on past land use and disturbances will be similar among the overstory tree species in this study because these sites were established under the same conditions and in a local area, thus controlling for climate, soil type, slope and aspect (Fisher 1995).

La Selva is considered a wet tropical forest (Holdridge 1967). Old-growth forest occupies 55% of La Selva's 1,536 hectares. Other land use includes moderately logged forest (7%), secondary forest (11%), early successional pasture (18%), and abandoned plantations (8%) (Hartshorn and Hammel 1994). In 2013, more than 160 families and 2000 species were known to occur at La Selva, according to the La Selva Florula Digital database (https://sura.ots.ac.cr/florula4/index.php). Woody vegetation comprises at least 45% of species found at La Selva (Hartshorn and Hammel 1994).

Experimental Setting

Fisher (1995) described previous land use of the experimental site and the experimental design for the plantations, summarized as follows. The experimental site was old-growth forest until ~1955 when the forest was cut and burned to clear land for cattle grazing. The pasture was abandoned in 1987, and then purchased by the Organization for Tropical Studies. The experiment was initiated in 1988 after preparing the 12-ha site by cutting and burning the grass thatch. The randomized complete block design contained 11 treatments (single species of trees) plus one control (no trees planted), replicated in four blocks (Figure 2-1). Each 50-×-50-m plot was divided into four quadrants for subsampling within plots. Trees were planted at a spacing of 3 × 3 m. Some species were thinned in 1991. Understory vegetation was cut during the first three to four years until the planted trees attained canopy closure (Haggar et al. 1997, Powers et al. 1997). By 2014, 26 years later, only four native overstory tree species of the 11 originally planted were alive in all four blocks: *Hieronyma alchorneoides* Allemão, *Pentaclethra macroloba* (Willd.) Kunth., *Virola koschnyi* Warb., and *Vochysia guatemalensis* Donn. Sm. Hereafter, the overstory tree species plots are referred to by genus, or by four-letter acronyms Hial, Pema, Viko and Vogu, respectively. One plot of *Vochysia* was not used in this study because a lightning strike on 31 October 2011 killed many of the overstory trees, thus making it incomparable to other plots.

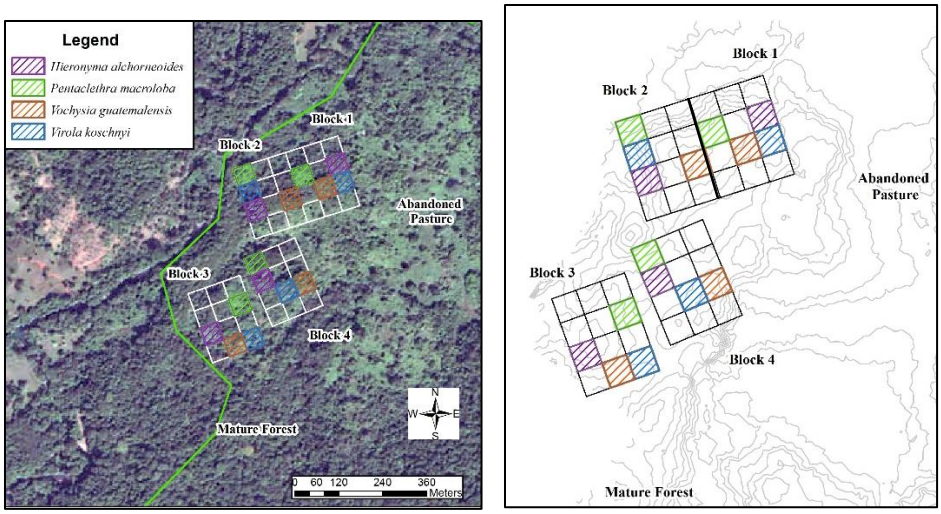

Figure 2-1. Randomized complete block design for experiment at La Selva Biological Station, Costa Rica using Quick Bird Imagery from 2003. Right image has 5 m contours.

Overstory Tree Species Descriptions

The four native overstory tree species differ in several traits that could influence seed rain of both wind- and animal-dispersed seeds (Table 2-1). *Hieronyma* and *Virola* provide fruit resources that attract animals. Although *Vochysia* seeds are wind-dispersed, they are also predated, especially by parrots. Though parrots are seldom dispersers, they might alter the behavior of other potential animal dispersers within *Vochysia* plots. *Pentaclethra* is a nodulated legume and the dominant tree in the old-growth forest of La Selva, with estimates of species density reaching 50% (Flores 2002). *Pentaclethra*'s autochorous seeds lack predators due to their high alkaloid and amino acid content (Anhalzer et al. 2010). Given its dense, monolayer canopy, *Pentaclethra* also provides a habitat resource as a shadier environment where howler monkeys rest during the day (Oberbauer and Strain 1985). Its nyctinastic leaves, which close at night, create a temperature microclimate in old-growth forest that is similar to that of secondary forests, given its dominance (Hirai et al. 2014).

Table 2-1. Traits of the four native overstory tree species in experimental plots at La Selva.

Tree species	Fruit[a]/Seed[b]	Seed length	Dispersal Mode	Crown Type	Resource
Hieronyma alchorneoides	 (b)	3 mm	Mammals and Birds	Deep, dense, conical[1]	Fruit
Virola koschnyi	 (a) & (b)	19 mm	Mammals and Birds	Deep, dense, conical[1]	Fruit
Pentaclethra macroloba	 (b)  (a)	40 mm	Mechanical	Dense, mono-layer[2]	Shade/habitat
Vochysia guatemalensis	 (a)	23 mm	Wind	Deep, dense, round[1]	Food source for parrots and macaws

Source:[1] Zamora and Montagnini 2007; [2]Hartshorn 1983

Overstory Tree and Woody Understory Measurements

Tree diameters, height, density, biomass, and leaf area index (LAI) in the plots were determined as described in Russell et al. (2017). Briefly, during annual tree species inventories, the diameter at breast height (dbh) and height of all trees and shrubs ≥10 cm dbh were measured in every plot. Naturally regenerating trees and shrubs <10 cm dbh and >2.5 m tall were inventoried annually in transects within the plots. Aboveground biomass and LAI were calculated from the dbh and height measurements, using biomass regressions developed from species-specific biomass harvests. For each of the four planted species, nine trees were harvested, and for the four most common understory species, 3-12 trees or shrubs were harvested.

Biomass of non-woody vegetation was determined in 2013 from destructive harvests of all vegetation within four randomly located 0.5 × 1.0 m quadrats per plot. Total aboveground biomass included the planted tree species plus all other vegetation except epiphytes. For this study, we used the annual inventory data from 2014-2015 to determine

whether species found in the seed rain were also regenerating within the overstory tree species plots or were immigrating into the plots.

Seed Trap Design and Placement

The seed traps in this study were 1.3 × 0.4 m for a sample area of 0.52 m^2. The seed trap was elevated with a rectangular polyvinyl chloride (PVC) frame and a removable mesh liner attached with clamps. Seed traps are generally elevated slightly above the forest floor to avoid seed decomposition and removal by ground animals of seed rain. This type of seed trap captures fruits and seeds falling from adult plants and those handled (defecated or dropped) by volant animals, but does not measure secondary dispersal, such as scatter or larder-hoarding, by ground-dwelling animals. Traps were levelled during installation so that all traps sampled the same projected area ~15 cm above the forest floor in this hilly site. Seed rain was collected at approximately weekly intervals for 14 months from 13 January 2014 to 9 March 2015. Unfortunately, seed rain could not be collected in the adjacent old-growth forest for logistical reasons.

One seed trap was placed at a randomly selected location in each of the four quadrants per plot (Figure 2-1). One quadrant was randomly selected for a fifth trap, for a total of five traps per plot. Traps were not placed within 3 m from the edge of each plot to reduce the possibility of edge effects. With five traps per plot in all four species in all blocks, the total number of seed traps was 75. We used two different mesh sizes of liners in the seed traps. In two of the five seed traps per plot, the trap was lined with 1-mm nylon mesh screen. Given the establishment history of the plantations, we anticipated that a reasonable amount of the seed rain would be from small-seeded, earlier successional woody species, which could pass through the standard 1-mm mesh size used for seed traps. To capture seeds smaller than 1 mm, we lined three of the five traps per plot with a tight-mesh polyester fabric, Terylene®.

Seed Collection and Identification

Seed-rain trap liners were removed from each trap, placed in Ziploc® bags, and transferred to the lab. Trap contents were inspected to remove immature seeds, fruit and their fragments without mature seeds. Trap liners were transported to the lab and immediately unfolded carefully on a clean lab bench. To remove seeds caught on large detritus within the trap, we rinsed the detritus with deionized (DI) water, and collected the rinsate in a beaker, from which we removed, counted, and recorded seeds and fruits recognizable to the naked eye. For the fine-mesh lined traps only, we scraped the remaining material, consisting of unidentified seeds and detritus, onto pre-folded filter paper, and rinsed it with DI water over sieves to catch seeds rinsed free from the detritus. We consolidated the seeds on the sieves with those on the filter paper and transferred the sample to petri dishes containing sand to start germination trials to determine the seeds' species. We placed the petri dishes in a shadehouse situated in a clearing near La Selva's laboratory and checked weekly for germination for one month. Seeds were identified to the lowest taxonomic level possible (generally, species or genus) based on the seedling. Unidentified large seeds were also germinated and identified based on the seedling. Seed samples, germinated plants, and their photos are archived at La Selva.

Seed Traits

A sample ranging from one to over 50 seeds of each species was cleaned to obtain fresh mass, length, width, and dry mass. If seeds were too small to be weighed singly, multiple seeds were weighed to obtain a mean mass across all seeds. Mean length and width were recorded for small seeds. Samples were placed in paper bags and dried at 65°C for approximately three days prior to dry mass measurement. For all seeds, we measured length from two points plus width. We supplemented our seed measurements with seed data from

other studies at La Selva (Letcher 2008, Wendt 2014). We used our data if available over other sources, but incorporated other studies in which maximum rather than mean measurements were made. We followed Wendt (2014) in assigning seed size categories: small ($\leq$ 6 mm); medium (6 < x < 15 mm); and large ($\geq$ 15 mm).

In addition to seed size based on our seed-trap data, we included information on the dispersal mode, life form, and successional status of species in seed rain based on other studies at La Selva (APPENDIX A.). We classified species by their dispersal mode, either biotic (animal) or abiotic (wind and mechanical), and life form of tree, liana, shrub, or palm according to Vargas (2000), Letcher (2008), Wendt (2014), S. Letcher (*pers. comm*. 2018), and the La Selva florula digital (https://sura.ots.ac.cr/florula4/) (APPENDIX A.). There was only one mechanically dispersed species in the seed rain, *Apeiba membranacea*, found within *Hieronyma* and *Vochysia*.

Data Analyses

The sample unit was the plot, so we summed seed rain data over the five traps within a plot over the 12 months. For these analyses, we did not include seeds of the planted overstory tree species within their own plot because we were interested in the composition of the seed rain arriving into the plots. We did not convert the 12-mo long data set to an annual basis because that would have biased the annual estimates, given that seed rain was very low in January through March (APPENDIX B.) (Figure 2-2). To achieve equal representation of each month within the year, seed rain was calculated on an annual basis, using data collected from 24 Feb 2014 through 23 Feb 2015. All analyses were done in R-version 3.3.3 (R Core Team 2018). Tukey HSD comparisons were done for pair-wise tests when appropriate with a significance of $P < 0.05$ using the package lsmeans (Lenth 2016). Figures were created in excel and the package ggplot2 in R (Wickham 2009).

In preliminary analyses, we considered the potential of spatial correlation in the data due to variation not captured in the randomized complete block design. We examined variograms and bubble plots for our responses of species richness, abundance and Shannon-Weiner diversity using the package sp in R (Pebesma and Bivand 2005). We found no apparent correlation (APPENDIX C.) and therefore, did not include spatial variables aside from block identity in our models.

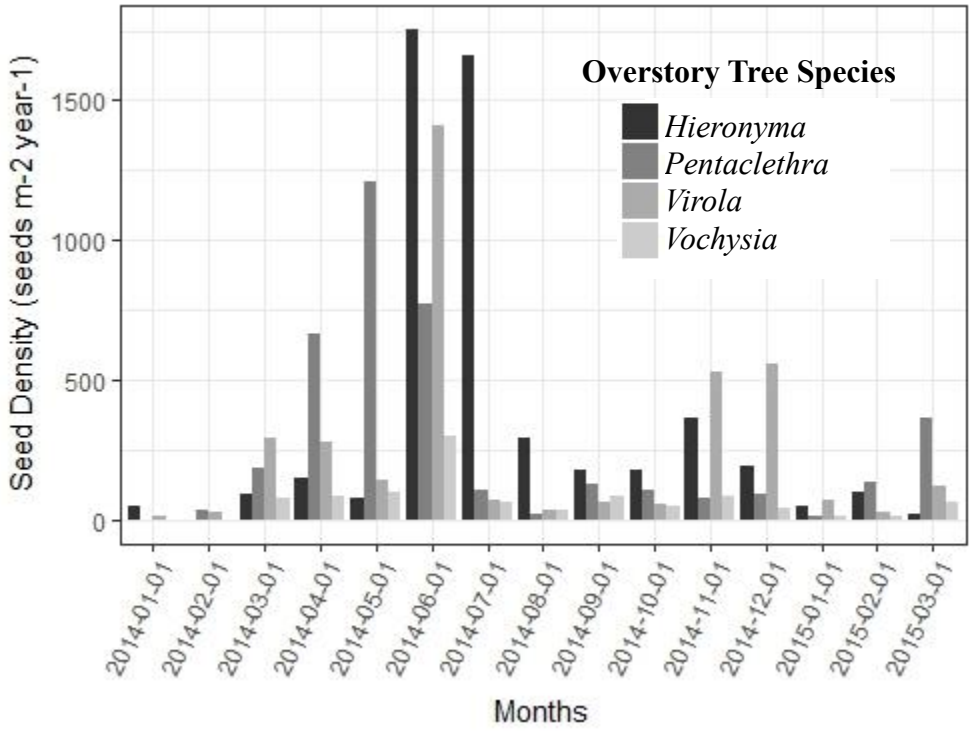

Figure 2-2. Total seed density over 14-month collection period.

Overstory tree species analyses

To analyze differences in abundance of seeds per plot across the four overstory tree species, we used a generalized linear mixed-effects model for overdispersed count data. Errors were modeled with a log-normal Poisson mixture, which was implemented by including a plot-specific random effect in the model below. This was fit using glmer() in the lme4 package in R (Bates et al. 2015) with a Laplace Approximation.

$$y = \text{Overstory tree species} + \text{Block} + (1|\text{plot}) + \text{Error}$$

To analyze differences in species richness and Shannon-Weiner diversity of seed rain across the four overstory tree species, we used linear models which were fit using lm() in the stats package in R (R Core Team 2018). We used the package vegan to determine species richness, Pielou's Evenness and Shannon-Weiner diversity index (Oksanen et al. 2017).

$$y = \text{Overstory Tree Species} + \text{Block} + \text{Error}$$

To analyze for differences in species composition of the seed rain across the four overstory tree species, a permutational analysis of variance (PERMANOVA) was used that incorporated differences across blocks and tree species. We used the packages geomorph and vegan in R to perform these analyses and the following ordinations (Adams and Otarola-Castillo 2013, Oksanen et al. 2017). The function advanced.procD.lm in the package geomorph was used to evaluate pairwise differences between overstory tree species (Collyer et al. 2015). Non-metric multidimensional scaling (NMDS) with the Bray-Curtis similarity coefficient was used to visualize the differences in community composition based on abundance distance measures. Because tropical rainforests commonly have many rare species, we also used a PERMANOVA with a Jaccard (presence/absence) distance metric. The Jaccard metric is a qualitative metric used to determine if species present in the seed rain differed among overstory tree species whereas the Bray-Curtis metric is quantitative and signals if the community structure of seed rain differs among overstory tree species (Pontash and Brusven 1988). Similarly, we visualized the differences in species composition across the four overstory tree species graphically through NMDS. We used a two-dimensional model because the stress was < 0.10 (Clarke 1993).

Trait analyses

For the seed-rain species trait analyses we analyzed each dispersal mode and life form separately to evaluate differences in seed rain across the four overstory tree species. We analyzed the responses of total seed rain abundance, species richness, Shannon-Weiner diversity and species composition using the models and packages described previously. For example with abundance, we analyzed for differences in abundance of animal-dispersed seed rain, abiotically dispersed seed rain, tree seed rain, shrub seed rain and liana seed rain across the four overstory tree species, each with a generalized linear mixed effects model using the glmer() package in R (Bates et al. 2015).

We examined general trends in successional status and seed size of species in the seed rain across the four overstory tree species plots. Because successional status is not particularly well defined, we applied Chazdon's approach for categorizing tree species, which includes relative abundance of species, including rare species, in different habitats while also allowing for unbalanced sample sizes (Chazdon et al. 2011). For liana species, we used Letcher's (2008) classifications from previous research conducted at La Selva.

To evaluate whether structural traits differed among overstory tree species, we used linear models incorporating the randomized complete block experimental design. These models were fit using lm() in the stats package in R (R Core Team 2018). The specific response variables included dbh, height, LAI, density, aboveground overstory tree species biomass and total aboveground biomass. These data were collected and calculated as described above in the overstory tree and woody understory measurements section according to Russell et al. (2017).

Results

Seed Rain Characteristics

Over the 12-month period, we collected 133,355 seeds from 121 woody species representing 41 families (APPENDIX B.). Nine species were identified to the genus as morphospecies. Nineteen seeds (0.01%) were not identifiable. Most species in seed rain were rare, with 50% of the species represented by ten or fewer seeds, whereas ten species accounted for 93% of all seed rain collected. Nine of the 10 most abundant species in the seed rain were animal dispersed. According to life form, shrub seeds comprised 65% of the total seed rain abundance and 36% of the species in the seed rain. Melastomaceae had the most species (19) of any family and the largest proportion of total seeds (46%). Only 26 large seeds (≥ 15 mm) were found in seed rain from 10 species while the five most abundant small-seeded species (≤ 6 mm) comprised 80% of total seed rain abundance (APPENDIX D.).

The most common life form in the seed rain was shrub, except in *Hieronyma* plots, where trees dominated (Table 2-2). The proportions of the various dispersal modes of the species arriving in seed rain were similar among the four overstory tree species (Table 2-2). Seed rain for animal-dispersed species had two peaks, from March through July, with a smaller peak in November and December. Seed rain of abiotically dispersed species peaked only in the month of April. Very few old-growth species of palms, trees and lianas occurred in any of the four overstory tree species plots. The next greatest proportion was of secondary species, with generalist species occupying the largest fraction (Table 2-2).

Table 2-2. Seed rain in four overstory tree species in experimental site at La Selva. Abundance expressed as percentage of total seed rain according to traits, species richness, and density as seeds m^{-2} y^{-1}.

			Hieronyma			***Virola***			***Pentaclethra***			***Vochysia***			***Total***	
			% of Total	**Richness**	**Density**	**% of Total**	**Richness**	**Density**	**% of Total**	**Richness**	**Density**	**% of Total**	**Richness**	**Density**	**Richness**	**Density**
Life form	*Tree*		80.6	40	4095	45.6	35	1606	43.4	30	1527	37.3	34	351	48	7579
	Shrub		14.6	29	742	51.6	27	1816	54.3	21	1911	48.6	20	458	44	4926
	Liana		4.7	10	237	2.6	13	91	2.3	11	80	13.4	14	126	21	534
	Palm		0	1	<1	0	1	<1	0	2	<1	0	2	<1	4	1
	Unknown		0.1	2	5	0.2	3	6	0	4	2	0.7	2	7	4	19
Dispersal mode	*Animal*		98.3	68	4990	94.1	67	3313	97.3	56	3426	92.8	60	874	103	12603
	Wind		1.7	13	88	5.9	12	206	2.7	12	93	7.1	11	67	17	454
	Mechanical		0	1	<1	0	0	0	0	0	0	0.1	1	<1	1	1
Life Form by Successional Stage	Liana	*Generalist*	3.4	7	175	1.6	10	56	1.7	8	60	8.8	8	942	15	1232
		Secondary	1.2	3	62	1	3	35	0.6	3	20	4.5	4	43	4	160
		Old growth	0	0	0	0	0	0	0	0	0	0	2	<1	2	0
	Tree	*Generalist*	2.7	7	138	7.9	6	277	30	7	1056	13.6	7	128	8	1600
		Secondary	75.2	19	3820	35.6	17	1251	10.1	14	357	19.5	17	183	20	5611
		Old growth	0	3	<1	0	3	<1	0.1	1	2	0	0	0	5	3
		Unknown	2.7	11	136	2.2	9	77	3.2	8	112	4.2	10	40	15	365
	Palm	*Old growth*	0	1	<1	0	1	<1	0	2	<1	0	2	<1	4	1
	Shrub	*Unknown*	14.6	29	742	51.6	27	1816	54.3	21	1911	48.6	20	458	44	4927
	Genus	*Unknown*	0.1	2	5	0.2	3	6	0	4	2	0.7	2	7	4	20
Seed size	*Small: ≤ 6 mm*		94	55	4776	98.3	56	3456	97.9	43	3446	91.8	47	865	75	12534
	Med.: 6 - 15 mm		5.9	22	302	1.7	20	60	2.1	23	74	8	20	75	36	511
	Large: ≥ 15 mm		<1	4	<1	<1	3	<1	<1	2	<1	<1	5	1.5	10	3

Effect of Overstory Tree Species on the Seed Rain

Overstory tree species differed in their effects on the abundance, species richness, and composition of the seed rain (Tables 2-2, 2-3, 2-4). We found no significant differences among the four overstory tree species in the abundance of seed rain, although *Vochysia* plots consistently had the lowest abundance. There were significant differences among overstory species in species richness of the seed rain ($P = 0.008$, df = 8, F = 8.2), with *Pentaclethra* plots having significantly lower species richness than *Hieronyma* plots. We found no difference among the four overstory tree species in Shannon-Weiner diversity index of seed rain ($P = 0.156$, df = 8, F = 2.3) or Pielou's Evenness ($P = 0.216$, df = 8, F = 1.9) (Figure 2-3). Seed rain composition varied among overstory tree species however, based on both the abundance-weighted Bray-Curtis ($P = 0.05$, $R^2 = 0.216$, F = 1.1, stress = 0.0936) and unweighted Jaccard ($P = 0.003$, $R^2 = 0.250$, F = 1.2, stress = 0.165) distance metrics (Figure 2-4). Based on the Bray-Curtis metric, there was a significant difference in community structure between *Pentaclethra* and *Vochysia* ($P = 0.026$), whereas with the Jaccard metric, there were significant qualitative differences between *Pentaclethra* and *Vochysia* ($P = 0.034$), *Hieronyma* ($P = 0.003$), and *Virola* ($P = 0.048$).

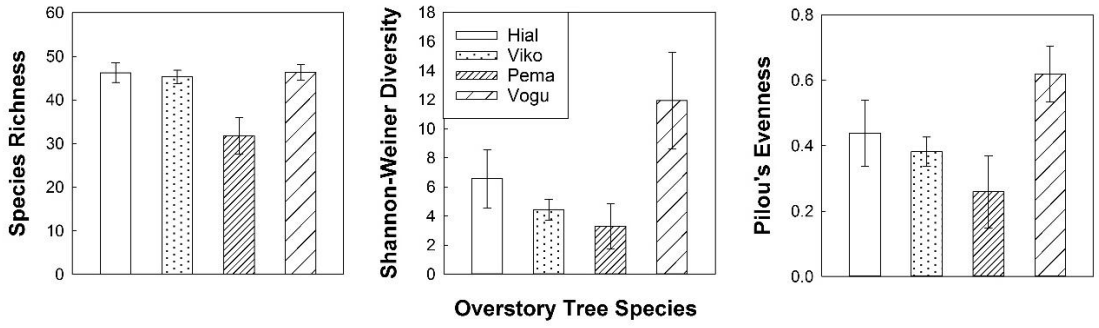

Figure 2-3. Diversity measures for annual seed rain in four overstory tree species (mean ± SE).

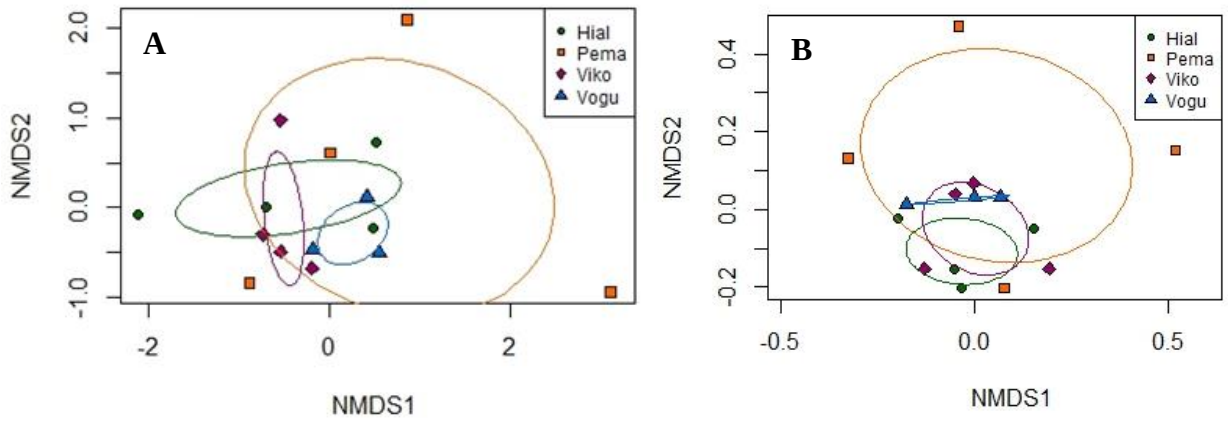

Figure 2-4. Non-metric Multidimensional Scaling two-dimensional ordinations of species composition of seed rain across four overstory tree species (15 total plots) with Bray-Curtis (A) and Jaccard (B) similarity coefficients.

Variation in Seed Rain Traits

Dispersal mode

We analyzed for differences among the four overstory tree species in dispersal modes of species arriving in the seed rain. *Pentaclethra* had significantly fewer animal-dispersed species in the seed rain than *Hieronyma* ($P = 0.03$, t = 3.6), *Virola* ($P = 0.03$, t = 3.5) and *Vochysia* ($P = 0.047$, t = 3.3) (

Table 2-3). There were no significant differences in abundance of animal-dispersed seeds, diversity, or composition among the four overstory tree species (

Table 2-3). We found significant differences in the composition of abiotically dispersed seed rain according to the Bray-Curtis metric, but not the unweighted Jaccard metric (

Table 2-3). This implies that the community structure of seed rain differed with abiotically dispersed species while the abiotically species themselves from a qualitative perspective did not differ significantly among overstory tree species. We also found no

significant differences among the overstory tree species in abundance, species richness or diversity of the abiotically dispersed seed rain (

Table 2-3).

Life form

Generally, species richness of trees in the seed rain accounted for the most differences among the four overstory tree species plots. Species richness of tree species in the seed rain was significantly different among the four overstory tree species (

Table 2-3), with *Pentaclethra* plots containing significantly fewer tree species (P = 0.0018). We found no significant differences in the abundance of seeds, or Shannon-Weiner diversity for any of the life forms among the four overstory tree species. The composition of liana and shrub seeds arriving as seed rain did not differ significantly among four tree species; however, tree species seed composition did differ (P = 0.024). *Pentaclethra* had significant differences in tree seed composition compared with *Hieronyma* (P = 0.046) and *Vochysia* (P =0.028) by the Bray-Curtis distance metric.

Table 2-3. Results of ANOVA and PERMANOVA analyses for traits of seed-rain species

		Abundance	*Richness*	*Diversity*	*B-C Comp.*	*Jaccard Comp.*
Dispersal Mode	Animal	P = 0.14 F = 2.53	P = 0.02* F = 6.10	P = 0.12 F = 2.68	P = 0.078 F = 1.04	P = 0.003* F = 1.26
	Abiotic	P = 0.18 F = 2.20	P = 0.63 F = 0.60	P = 0.19 F = 2.0	P = 0.01* F = 2.00	P = 0.143 F = 0.98
Life Form	Liana	P = 0.10 F = 3.06	P = 0.08 F = 3.14	P = 0.30 F = 1.42	P = 0.13 F = 1.06	P = 0.045* F = 1.22
	Shrub	P = 0.81 F = 0.32	P = 0.37 F = 1.21	P = 0.65 F = 0.56	P = 0.15 F = 1.00	P = 0.051 F = 1.10
	Tree	P = 0.17 F = 2.22	P = 0.01* F = 7.44	P = 0.32 F = 1.37	P = 0.07 F = 1.09	P = 0.01* F = 1.29

Successional status

Successional status of the seed rain did not differ among the four overstory tree species. *Vochysia* was the only tree species with that received old-growth, late-successional liana seeds. Generalist liana species comprised most of the liana seed rain, followed by secondary liana species, across all four overstory tree species (Table 2-2). Of the tree species in the seed rain, secondary species had the greatest seed density and species richness in the animal-dispersed overstory tree species (*Hieronyma* and *Virola*). In *Pentaclethra*, the greatest number of species in seed rain were secondary tree species, but generalist tree species had higher seed density (Table 2-2). Only five old-growth, animal-dispersed tree species arrived in seed rain across the entire study site, with none arriving in *Vochysia*, one in *Pentaclethra* and three each in *Hieronyma* and *Virola*, the two animal-dispersed tree species. These species arrivals in the seed rain were very sporadic and localized, with capture usually occurring in the same trap during multiple sampling periods.

Seed Size

Small-seeded species were over seven times more common than larger-seeded species in the seed rain (Table 2-2). The relative proportion of medium-seeded species was consistent among overstory tree species plots; however, the species composition differed. *Hieronyma* contained four times the density of medium-sized seeds than was found in any of the other overstory tree species plots (Table 2-2).

Overstory Tree Species Structural Traits

Tree density and height differed significantly ($P < 0.05$) (Figure 2-5). *Hieronyma* had the lowest tree density (281.64 ± 6.68 stems/ha) ($P = 0.013$) and *Pentaclethra* had the highest density (462.96 ± 31.34 stems/ha). *Pentaclethra* had the shortest height (16.02 ± 2.20 m) and *Vochysia* was tallest (23.91 ± 2.06 m) ($P = 0.029$). Other measurements of structure did not

differ, including dbh (P = 0.15), LAI (P = 0.18), aboveground biomass of the four overstory tree species (P = 0.135), and aboveground biomass for all plants (woody and non-woody) (P = 0.0721).

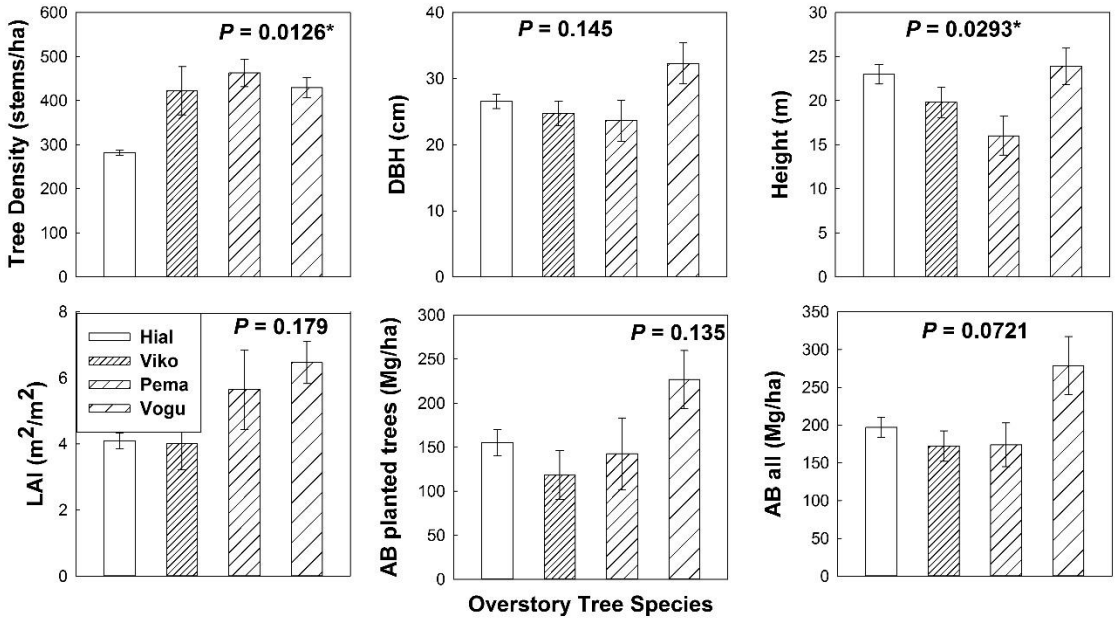

Figure 2-5. Structural traits of overstory tree species. Tree density includes only planted trees, DBH and height are means for all planted trees at the plot level. AB all includes the biomass of all plants found in the plot.

Immigrating Seed-rain Species

We compared woody species composition in the seed rain (across all plots) with woody species already occurring within the plots, as determined from annual surveys of established woody vegetation (entire plots for individuals ≥ 10 cm dbh and transects for those < 10 cm dbh). Of the total species arriving in seed rain, 47% did not occur in our annual inventory in 2013 (Table 2-4). Thus, we inferred that incoming seeds had originated from outside the plots, hence were immigrating. This is a conservative estimate, because it is unlikely that all the established species documented in the annual inventories were reproducing. Compared with tree species captured in seed rain, there were double to triple the

number of shrub species found immigrating into the plots (Table 2-4). Of those species immigrating into plots in the seed rain, 86% were animal dispersed and 14% were wind dispersed, similar to the general trends for species captured in seed rain that were not already present in the plots. No palm species arrived in seed rain that were not already present in the plots (Table 2-4, 2-4). Seed density was 10 times lower for species immigrating into plots in the seed rain (Table 2-5). Abiotically dispersed overstory tree species contained a relatively higher density of species arriving in seed rain compared with biotically dispersed species (Table 2-5).

Table 2-4. Species richness by life form in seed rain from immigrants and percentage of total species richness for that life form within each overstory tree species plot.

	Hieronyma		***Virola***		***Pentaclethra***		***Vochysia***	
Life form	Richness	% of total	Richness	% of total	Richness	% of total	Richness	% of total
Tree	8	20%	5	14%	6	20%	7	21%
Shrub	19	66%	20	74%	12	57%	12	60%
Liana	5	50%	8	62%	6	55%	9	64%

Table 2-5. Seed-rain density by life form of species immigrating into each of the four overstory tree species plots and percentage of total for that life form within each species plot. Units are seeds m^{-2} y^{-1} and percentage of total seed rain density.

	Hieronyma		***Virola***		***Pentaclethra***		***Vochysia***	
Lifeform	Density	% of total	Density	% of total	Density	% of total	Density	% of total
Tree	31	0.76%	16	1.0%	106	6.9%	23	6.6%
Shrub	24	3.2%	48	2.6%	67	3.5%	60	13%
Liana	31	13%	13	14%	27	34%	28	22%

Discussion

Given that many factors influence spatial variation in seed rain, the process is difficult to predict accurately and is often treated as random or global from an ecological perspective. In a unique setting in which climate, soil, and other edaphic features were similar across four

replicated single overstory tree species plantations, we found that seed rain differed in species richness, taxonomic and functional composition among plots of the four overstory tree species.

Effects of Overstory Tree Species

The four overstory tree species included in our study varied in functional attributes that were correlated with species composition and species richness of seed rain. Three of the overstory tree species (*Hieronyma, Vochysia* and *Virola*) that provided food for animals, had seed rain with significantly greater species richness of animal-dispersed species than plots with *Pentaclethra*, the overstory species that provided only a habitat resource. This supports our predictions but in unexpected ways because *Vochysia* is wind dispersed. *Vochysia* fruits are predated however. This Al-accumulating species has relatively high stocks of cations in its biomass, up to two times more Ca and 2-3 times more K, Mg, and Mn than the other three overstory tree species (Russell et al. 2017). We have only limited data for fruits (data unpub.), but they support this cation-concentrating tendency of *Vochysia.* This higher cation nutrition in *Vochysia* fruits could explain their attraction to certain seed predators. Calcium is a nutritional requirement for parrots that is often limited in the environment (Koutsos et al. 2001, Matuzak et al. 2008). *Vochysia* plots contained similar species richness and species composition in the seed rain to the two animal-dispersed overstory tree species which is surprising given that parrots are not often suitable dispersers (Levey et al. 1994). It's possible that the presence of parrot species altered the behavior of other bird species that were potential dispersers through reducing the predation risk (Tellería et al. 2001). *Pentaclethra* plots contained significantly different species composition than the other three tree species. With the approximately 1,000 woody species in the nearby old-growth forest (La Selva Florula Digital), *Pentaclethra*, though dominant in the old-growth forest, received so few

species in the seed rain, and with such different composition. *Pentaclethra* seeds contain a chemical defense that is toxic to most animals and therefore would not attract potential animal dispersers into those plots. This indicates that overstory tree species influence their local neighborhood through dispersal filtering and that food resources are a critical factor for increasing seed rain into regenerating forests.

Additionally, we found the differences among the four overstory tree species were driven by the quantity of animal-dispersed tree and liana species arriving in the seed rain. This is consistent with the general finding that for tropical rainforests, animal-dispersal is the most common dispersal mode for woody species and thus, if sites are not attractive to dispersers, there will be fewer animal-dispersed species in the seed rain (Levey and Byrne 1993, Russo 2003, Russo et al. 2006, Côrtes and Uriarte 2012, Razafindratsima and Dunham 2015). *Pentaclethra* does provide habitat for Mantled howler monkeys *(Alouatta palliata*) but these species forage mainly on leaves and do not contribute substantively to local seed rain (Stoner 1996). By offering food resources, three of the four overstory tree species in this experiment were apparently influencing animal behavior, and in doing so, creating variation in seed rain.

Overstory tree species traits appeared to have influenced disperser behavior, thus driving differences in dispersal of animal-dispersed species (Slocum 2001, Troillet et al. 2017). Birds often prefer tree species with the highest canopy cover because it provides predator protection (Fink et al. 2009). *Pentaclethra* trees had the shortest height of the planted tree species. Furthermore, *Pentaclethra* canopies are often mono-layer whereas the other three overstory tree species provided deep canopies that may afford greater protection against predators for potential bird dispersers. Additionally, bird presence and species

richness tend to be negatively correlated with understory stem density (Reid et al. 2012), which could explain differences in animal-dispersed seed rain in our study.

Other studies have documented the effects of overstory tree species on filtering regeneration of saplings through establishment limitation (Parrotta 1995, Sansevero et al. 2011, Martínez et al. 2015). Our study indicated that filtering by overstory tree species occurs even sooner in the community assembly process, at the seed arrival stage. As such, the effects of individual overstory tree species on species composition of seed rain will have legacy effects on other local-scale processes including establishment and competition. The spatial variation in seed rain resulting from differences in the effects of individual overstory tree species has the potential to create unique neighborhoods from the time of seed arrival, thus providing a means for maintaining high diversity in tropical rainforests.

Consequences for Restoration and Community Assembly

Current restoration studies in the tropics have tested the effects of planting practices on woody regeneration including natural regeneration, the nucleation approach with tree islands, and plantations of mixed and single tree species (Bechara et al. 2016, Chazdon et al. 2016, Holl et al. 2011, 2017). In comparing effectiveness of these techniques at the local scale, the plantation approach resulted in similar species composition of tree recruits to that of reference forests whereas the nucleation and plantation approaches succeeded in increasing species richness and diversity, unlike the natural regeneration approach after 10 years (Holl et al. 2017). This study increases our understanding of dispersal filtering and neighborhood effects of the planted overstory tree species. Three of our study species are commonly used in restoration projects in Costa Rica: *Hieronyma, Virola* and *Vochysia* (Cole et al. 2010, Reid et al. 2015, Holl et al. 2017). Our results indicated that for tropical rainforests, in which the majority of woody species are animal dispersed, using a tree species

that provides food or habitat resources can increase the diversity of incoming seed rain (Cole et al. 2010). This study provides evidence for considering functional traits of the overstory tree species in restoration planning and design, as individual tree species can affect restoration success through filtering community composition in seed arrival (Hulvey and Aigner 2014).

In our study, large-seeded species were rare and mainly animal-dispersed. Larger seed size is typical of late-successional species; relatively larger quantities of endosperm provide a food source for the embryo, enabling it to overcome light and nutrient limitations in old-growth forests (Kitajima 2002, Baraloto and Forget 2007). Only two of the 10 large-seeded species were classified as late-successional species while other late-successional species, had medium and small seeds (six and two, respectively). Small-seeded species comprised over 91% of the seed rain in this study. Early-successional forests, where light is less limiting, tend to have more small-seeded species. Letcher (2008) found that young forests (early-successional) in this region had more lianas with small seeds, whereas larger-seeded, old-growth forest liana species may be absent because of missing dispersers (Dunn 2004). Our results show these experimental sites contained only two late-successional liana species that were animal dispersed in *Vochysia*, suggesting that dispersers may be lacking in the three other overstory tree species.

After 26 years of succession in these experimental plots, 47% of the species arriving in seed rain did not already occur within the plots. We infer that succession had not reached a steady state, such that the current differences among the four overstory tree species in species composition and species richness of the seed rain could continue to change. Although seed rain in *Hieronyma* contained more secondary specialist than generalist tree species, this was

the result of one prolific species captured within a single trap for a few sample dates. Otherwise, similar proportions of successional stages made up the seed rain across the four overstory tree species. In chronosequence studies, Wendt (2014) found that the number of smaller-seeded species decreased and large-seeded species increased with the age of the forest (Wendt 2014). Our results were consistent with this finding, and all four overstory tree species appeared to be on the same successional trajectories, despite differences in species richness and composition of the seed rain. The low number of late-successional species across our study site suggested that these regenerating plots would approach a community composition similar to that of nearby old-growth forests only very slowly, if ever.

Nevertheless, the potential for regeneration at this study site was high, given an annual seed-rain density ranging from 942 to 5,177 seeds m^{-2} $year^{-1}$ across the four overstory tree species. At slightly higher elevation sites in Costa Rica near Las Cruces Biological Station, seed rain densities in four-year old plantations were approximately 550 seeds m^{-2} $year^{-1}$ (Cole et al. 2010). Our study site was closer to old-growth forest than the plantations near Las Cruces, suggesting that the importance of the matrix within which the restoration site is initiated. La Selva forests likely served as important seed sources in our study. Time since establishment may also influence the effect of dispersal filtering by tree species in a restoration context (Reid et al. 2015).

We found that overstory tree species created local spatial variation in seed rain by filtering seed arrival. By influencing seed rain, we expect a cascading effect to occur, with local neighborhoods of different species compositions differing also in other processes such as competition, density-dependent processes, and interactions with pathogens and mutualists at the local scale. Additionally, this early filtering process will constrain which species are

able to successfully recruit to adulthood within a regeneration site. These results indicate that individual overstory tree species facilitate the maintenance of species richness in tropical forests through dispersal limitation as a filter in the dispersal process.

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CHAPTER 3. EFFECT OF MESH SIZE IN SEED TRAPS IN A TROPICAL RAINFOREST

Modified from a paper to be submitted to *Methods in Ecology and Evolution*

Bridgette D. Kirk[1,2], Ann. E. Russell[1], Sabrina Russo[3], Orlando Vargas[4], Ricardo Bedoya[5]

Abstract

1. Seed dispersal, a critical process that shapes plant communities, is most commonly quantified using seed traps to capture seed rain. The typical mesh size for seed traps is 1-mm, for reasons of time, cost and decay of samples. However, many tropical species have very-small seeds, < 1 mm in length or width. We addressed the questions of whether these very-small seeds would be captured in 1-mm mesh (regular) traps, and if not, how it would affect the inferences made. We compared the abundance, diversity, and composition of seed rain in regular- and fine-mesh (Terylene® fabric, 1 µm) seed traps in a species-rich tropical rainforest.
2. We collected seed rain for 12 months in both fine- and regular-mesh traps at La Selva Biological Station, Costa Rica. The split-plot experimental design included a wholeplot factor of overstory tree species in a randomized complete block design with a subplot factor of two mesh sizes in seed traps (n = 75 traps). We evaluated the seed rain total abundance, species richness, Shannon-Weiner diversity, Pielou's evenness, and species composition between the two mesh sizes.

[1] Department of Natural Resource Ecology and Management, Iowa State University, Ames, Iowa 50011 USA
[2] Primary researcher and author for correspondence
[3] School of Biological Sciences, University of Nebraska, Lincoln, Nebraska 68588 USA
[4] Organization for Tropical Studies, Puerto Viejo de Sarapiquí, Costa Rica
[5] Fondo Nacional de Financiamiento Forestal, Costa Rica

3. Across all traps, we collected 133,355 seeds from 121 woody species in 41 families. Abundance, species richness and diversity differed significantly between fine- and regular-mesh, with fine-mesh traps collecting on average 14 ± 1 (mean ± SE) more animal-dispersed species and 8 ± 1 more tree species per trap area than regular-mesh traps. Species composition varied between fine- and regular-mesh traps (Bray-Curtis and Jaccard similarity indices, $P = 0.001$ for both).
4. Seed traps are an important tool for characterizing seed arrival, and thus inferring the consequences of seed limitation on community assembly and restoration success, especially in tropical rainforests. The regular-mesh traps underestimated species richness by 50% and missed 90% of the very-small seeded species (< 1 mm). Considering that many early successional species were very-small seeded, the use of fine-mesh traps are critical for achieving the goal of assessing the successional status of seed rain species. Fine-mesh traps required five times more time and cost/effort, which may be impractical. The ineffectiveness of regular mesh in capturing very small seeds should be taken into account in interpreting results, however.

Introduction

Seed dispersal is a well-studied community assembly process that plays a key role in structuring plant communities (Traveset, Heleno, & Nogales 2014). Nevertheless, seed dispersal is hard to quantify accurately, in part because it is a highly stochastic process. The stage of seed dispersal, or the arrival of seeds in seed rain, is the first step in seedling establishment in plant communities (Schupp, 1993; Wang & Smith, 2002) and can strongly influence successional trajectories in regenerating secondary forests (Letcher, 2008). Accurately describing the composition of seed rain is a fundamental component for

evaluating mechanisms that structure plant communities and assessing whether niche-assembly versus dispersal-assembly processes predominate. For example, a biased estimate of seed rain composition may lead to conclusions that habitat filtering at the seedling stage is unimportant in determining patterns of species diversity in plant communities. It is therefore important to develop field methods that sample the seed rain in a comprehensive and unbiased way. Seed traps are commonly employed to assess local seed dispersal processes that may be of consequence for restoration efforts.

Seed traps measure seed arrival by passively capturing seeds that are dispersed (Stevenson & Vargas, 2008). Seeds differ in size, dispersal modes, and other features, and so the effectives of seed traps at capturing seeds depends on trap design. Seed traps can be designed to test specific hypotheses by capturing specific dispersal modes (Galindo-González, Guevara, & Sosa 2000; Morris, Raulings, Melbourne, Mac Nally, & Thompson 2011), or the community in general (Hardesty & Parker, 2003; Rother, Pizo, Siqueira, Rodrigues, & Jordano 2015). Most seed traps are designed to limit losses of captured seeds due to predation, wind, rain and bouncing (Kollmann & Goetze, 1998; Page, Newlands, & Eales 2002; Stevenson & Vargas, 2008). Common designs include bucket traps, sticky traps, hoop traps, circular hanging traps, funnel traps and mesh traps (Cottrell, 2004; Cole, Holl, & Zahawi 2010; Caves, Jennings, HilleRisLambers, Tewksbury, & Rogers 2013). The ideal seed trap should capture an unbiased sample of the seed rain, be affordable and easy to check, should not wear out in the environment and should drain water easily to prevent seed decay. Stevenson and Vargas (2008) found that traps made of mesh fabric suspended on polyvinyl chloride (PVC) pipe were the most effective design, with the least loss in mass and number of seeds due to the effects of wind and bouncing. The design has been used in

numerous studies in tropical rainforests, including long-term studies of seed dispersal (Wright, Calderón, Hernandéz, Detto, & Jansen 2016). Although the integrity, design and structural components have been well assessed (Rose, Stewart, Brinkman, Paxton, & Yelenik 2017), trap suitability for all seed sizes has received less attention.

In previous seed-trap studies in the tropics, the mesh sizes ranged from 0.13-mm to 2-mm (Russo, 2003; De Melo, Dirzo, & Tabarelli 2006; Zamora & Montagnini, 2007; Blackham, Thomas, Webb, & Corlett 2013; Wright, Calderón, Hernandéz, Detto, & Jansen 2016; Rose, Stewart, Brinkman, Paxton, & Yelenik 2017). While the sites for these studies varied in many environmental aspects, the goal of capturing all arriving seeds was similar. If the trap design fails to capture all sizes of seeds, it could influence the inferences made because seed size is correlated with many other plant functional traits, including dispersal mode, successional status, wood density, carbon storage and growth rate (Kitajima, 1994; Leishman, Wright, Moles, & Westoby 2000; Chazdon, Careaga, Webb, & Vargas 2003; Letcher, 2008; Osuri & Sankaran, 2016). Some studies documented consideration of mesh size in relation to regional seed sizes, whereas others acknowledged that seeds smaller than the mesh size were likely not captured (Dalling, Muller-Landau, Wright, & Hubbell 2002; Hardesty & Parker, 2003; Rose, Stewart, Brinkman, Paxton, & Yelenik 2017).

Seed traps are often used to determine whether dispersal limitation, or the failure of seeds to arrive, exists at a site (Svenning & Wright, 2005; Reid, Holl, & Zahawi 2015). Dispersal limitation can inform restoration practices in tropical rainforests by encouraging seed addition or seedling planting if a desired recruiting species is found to be seed limited. Seed traps can also be used to determine the trajectory of restoration of a secondary forest based on the successional status of species in seed rain (Letcher, 2008). Pioneer, early-

successional species are often very-small seeded (< 1 mm in width or length) and may not be captured by a seed trap with a mesh size of 1 mm (Chazdon, Careaga, Webb, & Vargas 2003). Thus, the results may indicate fewer early successional species are present and therefore that the site has reached a more advanced stage of succession.

We compared differences in seed rain captured in traps made using two mesh sizes of fabric, the commonly used 1 × 1 mm mesh and a fine-mesh fabric (Terylene®, 1 µm). We addressed the question of whether seed rain abundance, species richness, Shannon-Weiner diversity, Pielou's evenness and species composition differed between mesh sizes. We examined differences in functional attributes of species captured in seed rain and whether the species were already represented by established plants regenerating within the plots. We predicted that the traps made from the regular-mesh fabric would not capture very small seeds that are more likely to be from early successional tree species, compared with traps using finer mesh fabric. We also evaluated whether the effect of the mesh size in the seed trap differed among overstory tree species in which seed traps were situated. Finally, we considered how inferences and interpretations about seed dispersal and regeneration depend on the mesh size of the seed traps.

Methods

Study Site

This study was conducted in the Atlantic lowlands of Costa Rica at La Selva Biological Station (hereafter, "La Selva") (10° 26' N, 84° 01' W). La Selva's 1500 hectares are situated within a predominantly agricultural matrix that includes banana, pineapple and palm plantations, cattle pastures, and tree plantations. However, La Selva's old-growth forest is contiguous with Braulio Carrillo National Park that extends 3000 m upslope to the top of

Barva volcano. The experimental site is bordered on the north and west by the Peje River, on the east by abandoned pastures and on the south by old-growth forest within La Selva (Butterfield, 1994). Mean annual rainfall is 4000 mm and mean annual temperature is 25.8°C, with no distinct dry season (Sanford *et al.*, 1994). La Selva is considered a wet tropical forest (Holdridge, 1967). The topography is hilly, with mean elevation ranging from 40 to 100 m above mean sea level (Haggar, Wrightman, & Fisher 1997).

Old-growth forest is the dominant vegetation type, occupying 55.2% of La Selva. In 2013, more than 160 families and 2000 species of vascular plants occurred at La Selva (La Selva Florula Digital database, https://sura.ots.ac.cr/florula4/index.php). Woody vegetation comprises at least 45% of species found at La Selva (Hartshorn & Hammel, 1994).

Experimental Setting

Fisher (1995) described previous land use of the site and experimental design, summarized as follows. The site was old-growth forest until ~1955 when pasture was established for cattle. It was grazed until the pasture was abandoned in 1987. The experiment was initiated in 1988 after preparing the 12-ha site by cutting and burning the grass thatch. The original randomized complete block design contained 11 single tree species treatments plus one control in 50 × 50 m plots, replicated in four blocks (Figure 2-1). Tree species were assigned to plots in a stratified random manner, such that each species occupied each topographic position (hilltop, slope, and bottom of hill) across the four blocks. Trees were planted at a spacing of 3 × 3 m. Each plot was divided into four quadrants (25 × 25 m) for subsampling within plots. Some species were thinned in 1991. By 2014, 26 years later, only four overstory tree species (all native) were alive in all four blocks: *Hieronyma alchorneoides* Allemão, *Pentaclethra macroloba* (Willd.) Kunth., *Virola koschnyi* Warb., and *Vochysia guatemalensis* Donn. Sm. Hereafter, the species are referred to by genus. One

plot of *Vochysia* was not used in this study because a lightning strike in 2011 killed many of the overstory trees, thus making it incomparable to other plots.

Understory vegetation in these plots was cut during the first three to four years, until the planted trees attained canopy closure (Haggar, Wrightman, & Fisher 1997; Powers, Haggar, & Fisher 1997). After that time, understory vegetation was allowed to regenerate on its own. In annual surveys of the understory, the species, diameter at breast height (dbh) and height of non-planted woody species were recorded within the plots, as described in CHAPTER 2. of this thesis. In 2013, 40 woody species occurred in the understory. By 2013, regeneration understory biomass ranged from 19-31% of total biomass within the plots. These data provided a list of extant species in the understory. We used that list to differentiate between species in the seed rain that arrived from outside the experimental plots and those that could have originated from parents within the plots. This is a conservative estimate of immigrating species in the seed rain, given that we did not have genetic data to identify parents and progeny.

Seed Trap Design and Placement

We used a mesh-lined, seed trap, 1.3 × 0.4 m in area and 8 cm deep, to capture fruits and seeds falling from adult plants, dispersed by wind, and those handled (defecated or dropped) by volant animals. This method does not measure secondary dispersal by ground-dwelling animals that occurs after initial dispersal from the parent plant. Seed traps are generally elevated slightly above the forest floor to avoid decomposition of seed rain and reduce removal by ground dwelling organisms. Our traps were levelled during installation so that all traps sampled the same projected area ~15 cm above the forest floor at the lowest point in this hilly site.

One seed trap was placed at a randomly selected location in each of the four 25 × 25 m quadrants per plot. One quadrant was randomly selected to receive a fifth trap, for a total of five traps per plot. Traps were not placed within 3 m of the edge of each plot to reduce the possibility of edge effects. Two traps were lined with 1 mm nylon mesh screen, the size typically used in seed rain studies, hereafter referred to as 'regular' mesh. The other three traps were lined with a 1 µm tight-mesh polyester fabric, Terylene®, hereafter referred to as 'fine' mesh, for capturing all seeds, including those ≤ 1 mm. Mesh size was assigned to traps at random. With five traps per plot in all four species, the total number of seed traps was 75, 30 regular mesh and 45 fine mesh.

Seed Collection and Identification

Seeds in traps were collected approximately weekly for 12 months. Trap contents were inspected to remove immature seeds and fruit/fruit fragments containing no mature seeds. Seed-rain trap liners were then removed from each trap, placed in Ziploc® bags, and transferred to the lab. Trap liners were unfolded carefully on a clean lab bench. To remove seeds caught on large detritus within the trap, we rinsed the detritus with deionized (DI) water, and collected the rinsate in a beaker, from which we removed, counted, and recorded seeds and fruits recognizable to the naked eye. We scraped the remaining material, consisting of unidentified seeds and detritus, onto pre-folded filter paper, and rinsed it with DI water over sieves to catch seeds rinsed free from the detritus. We consolidated the seeds on the sieves with those on the filter paper and transferred it to petri dishes containing sand to begin germination trials to determine the species identification of unknown seeds. We placed the petri dishes in a shadehouse situated in the lab clearing at La Selva and checked for germination on a weekly basis for one month. Seeds were identified to the lowest taxonomic

level possible (generally, species or genus) based on the seedling. Seed samples, germinated plants, and their photos are archived at La Selva.

A sample ranging from one to over 50 seeds of each species was cleaned to obtain fresh mass, length and dry mass. If seeds were too small to be weighed singly, multiple seeds were weighed to obtain a mean mass across the seeds. Samples were placed in paper bags and dried at 65°C for approximately three days prior to dry mass measurement. We supplemented our seed measurements with seed data from other researchers at La Selva (Letcher, 2008; Wendt, 2014). Seeds were assigned to one of four seed size categories based on maximum measured length or width: very small (< 1 mm); small ($1 \leq x \leq 6$ mm); medium ($6 \leq x \leq 15$ mm); large (>15 mm).

Seed-rain Species Traits

In addition to seed size, we categorized species captured in seed traps according to other ecological traits including dispersal mode, life form and successional status. We classified species by their dispersal mode, either biotic (animal) or abiotic (wind and mechanical), and life form of tree, liana, shrub, or palm according to Vargas (2000), Letcher (2008), Wendt (2014), S. Letcher (*pers. comm*. 2018), and the La Selva florula digital (https://sura.ots.ac.cr/florula4/) (APPENDIX A.). Successional status could not be assigned to many of the shrub species.

Data Analysis

In this split-plot design, the whole plot treatment was the overstory tree species and the subplot was mesh size. Seeds of the experimental overstory tree species collected in seed traps within their own plot were not included in the analyses. To achieve equal representation of each month within the year, annual seed rain was based on samples collected from 24 Feb 2014 to 23 Feb 2015, as described in Chapter 2. All analyses were done in R-version 3.3.3 (R

Core Team, 2018). Tukey HSD comparisons were done for pair-wise tests when appropriate with a significance of $P \leq 0.05$ using the lsmeans and emmeans packages (Lenth, 2016; 2018).

We tested whether traps within a plot captured similar seed rain by analyzing the capture efficiency of mesh size in traps. Capture efficiency was defined as the proportion of seeds of each species captured in regular-mesh traps per total number of seeds collected in both mesh sizes for each species. Species were categorized into one of the four size categories based on seed length and width. We hypothesized that the regular mesh would capture a subset of the species captured in the fine-mesh traps, with a lower capture efficiency.

To analyze differences in abundance of seeds per mesh size, we used generalized linear mixed-effects model for the overdispersed count data. Errors were modeled with a log-normal Poisson mixture, which was implemented by including plot-specific and trap-specific random effects in the model below. The model was fit using glmer() in the lme4 package in R (Bates *et al.,* 2015) with a Laplace Approximation.

y = Overstory tree species + Block + Mesh size + Mesh size*Overstory tree species +

(1|Overstory tree species:Block) +(1|Trap) + Error

To analyze differences in species richness, Shannon-Weiner diversity, and Pielou's evenness of seed rain capture in two mesh sizes, we used linear mixed-effects models which were fit using lmer() in the stats package in R (R Core Team, 2018). We used the package vegan to determine species richness, Shannon-Weiner diversity index and Pielou's Evenness (Oksanen *et al*., 2017).

y = Overstory tree species + Block + Mesh size + Overstory tree species*Mesh size + (1|Overstory tree species:Block) + Error

We analyzed differences between regular and fine mesh in species composition of seed rain using permutational analysis of variance (PERMANOVA). We visualized these differences using non-metric multidimensional scaling (NMDS) with abundance-weighted Bray-Curtis and unweighted Jaccard metric. The Jaccard metric is a qualitative metric used to determine if species present in the seed rain differed between mesh sizes whereas the Bray-Curtis metric is quantitative and signals if the community structure of seed rain differs between mesh sizes (Pontash & Brusven, 1988). We used a three-dimension fit for the NMDS plots because the stress was too high for trustworthy interpretation in two-dimensional fit (> 0.2) (Clarke, 1993). We used the packages geomorph (Adams & Otarola-Castillo, 2013) and vegan (Oksanen *et al*., 2017) to perform these analyses, and packages ggplot2 (Wickham, 2009) and plotly (Sievert *et al*., 2017) to create the NMDS ordinations.

Because the area of collection was unequal for fine- and regular-mesh traps, we chose to find averages on a per trap basis, with the focus on alpha diversity. We determined trap averages for dispersal mode and life form of species found in each mesh size in the seed rain. Though the models above for abundance, species richness, Shannon-Weiner diversity and Pielou's evenness account for unequal trap size, these comparisons cannot fully account for differences in collection and this should be considered when interpreting results.

We evaluated differences between the two mesh sizes in terms of species immigrating into the plots in the seed rain according to dispersal mode and life form. We also evaluated the interaction between mesh size of the seed trap and the overstory tree species. The

response variables measured included abundance, species richness, Shannon-Weiner diversity, and species composition.

Results

Variation in the Species Composition of the Seed Rain

Over the 12-mo period, we collected 133,355 seeds from 121 woody species representing 41 families (APPENDIX E.). Total abundance of seed rain ($P = 0.001$, df = 62, z = -3.436) and species richness and diversity of the seeds in seed rain differed significantly between mesh sizes ($P < 0.0001$, df = 56, t= -21.5; $P < 0.0001$, df = 56, t = -5.6 respectively) but evenness did not ($P = 0.453$, df = 56, t = -0.7). With regard to species richness, regular-mesh traps captured 51% of the species arriving in seed rain in all traps, while the fine-mesh traps captured 90% of the species (APPENDIX F. APPENDIX E.). Of the 21 species with very-small seeds, we found only two of those species in the regular-mesh traps (APPENDIX G.), and seed from one of those two species, *Clidemia japurensis*, were found only in fruit within the regular mesh traps. For the other species, *Miconia affinis*, regular traps captured seeds, but they were not abundant, accounting for <3% of the total abundance for that species across all regular-mesh traps. All the very-small seeded species were animal dispersed and included one species of liana, two of trees, and 18 of shrubs (APPENDIX G.). With regards to abundance, the regular-mesh traps captured ~ 25% of seed rain across all seed sizes. Capture efficiency for regular-mesh traps decreased with seed size, from medium-sized (median = 39%) to very-small-sized seeds (median ~0%) (Figure 3-1). With only 26 large seeds from 10 different species, trends were not evident for large seeds. Capture efficiency for fine-mesh traps was more consistent across seed sizes with a median of 100% for all sizes except medium (median = 60%) (Figure 3-2). Species

composition of seed rain varied significantly between mesh sizes based on both Bray-Curtis (P = 0.001, stress = 0.15, R^2 = 0.04, F = 4.5) and Jaccard (P = 0.001, stress = 0.15, R^2 = 0.17, F= 18.8) similarity indices (Figure 3-3).

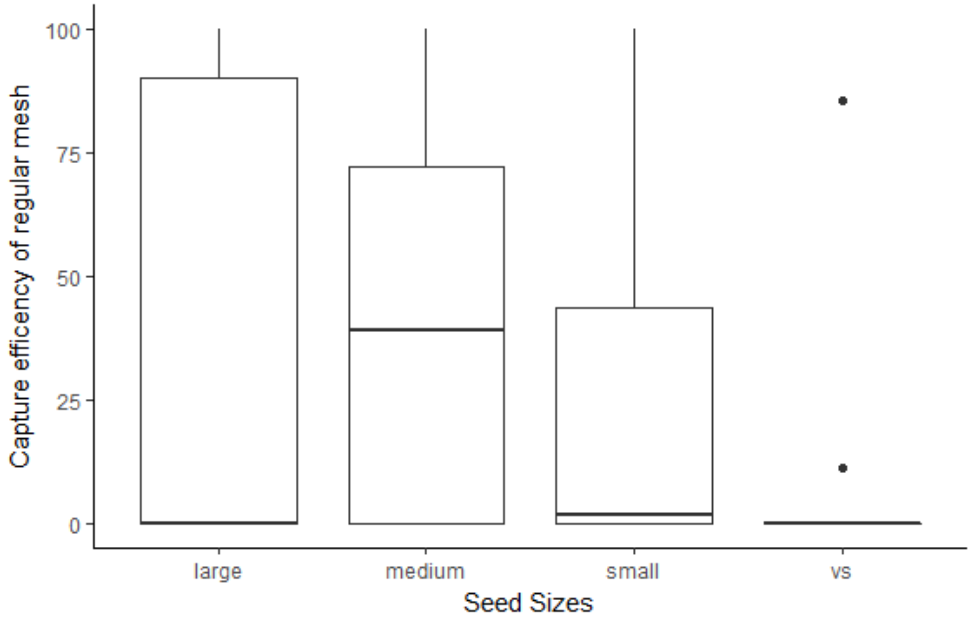

Figure 3-1. Capture efficiency of regular mesh traps (1 × 1 mm) as a percentage of total seeds captured of each seed size category.

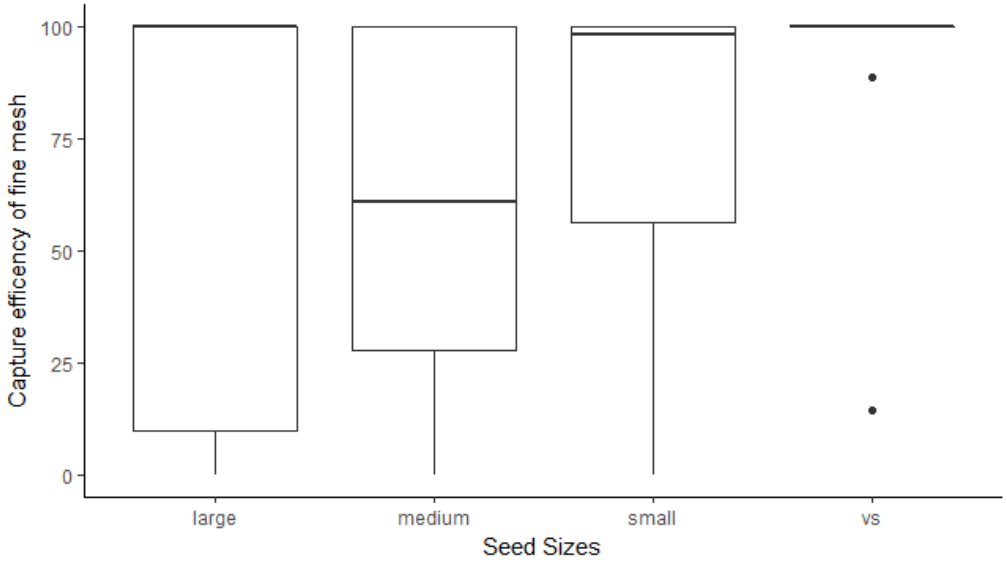

Figure 3-2. Capture efficiency of fine mesh traps (1 µm gauge) as a percentage of total seeds captured of each seed size category.

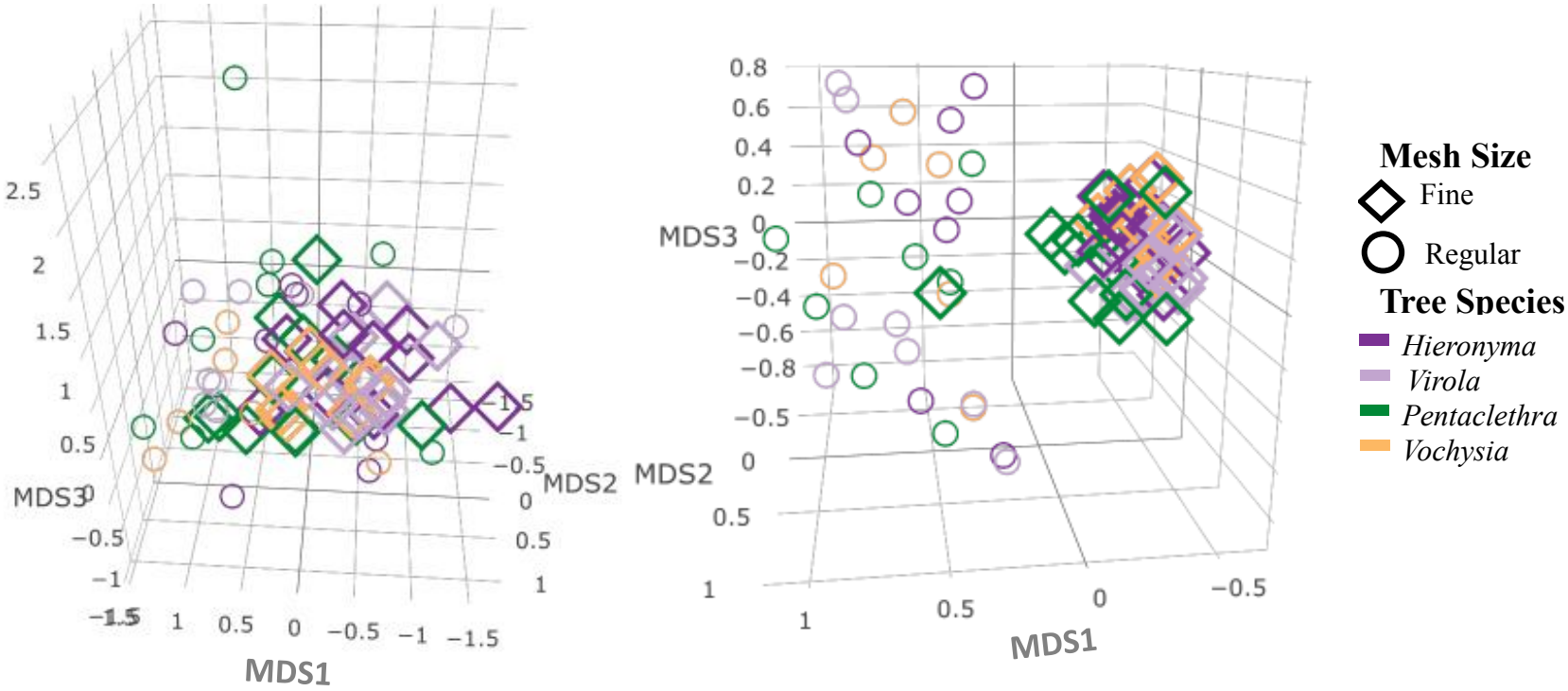

Figure 3-3. Species composition of seed rain captured in two different mesh sizes visualized with Non-metric Multidimensional Scaling 3D ordinations with Bray-Curtis (left) and Jaccard (right) metrics.

Functional Attributes of Seed Rain

We characterized the species captured in seed rain and compared the functional attributes of the species collected in the two mesh sizes. The proportion of species dispersed by animal, wind, or mechanically were similar between regular and fine mesh (Table 3-1). Seeds of tree species comprised a greater proportion of the total seeds in regular than in fine mesh (Table 3-1). Compared with fine-mesh traps, the regular-mesh traps captured 3% of the total abundance of old-growth species across all lifeforms and 50% of the old-growth species in the seed rain (Table 3-1). Fine-mesh traps captured 14 more animal-dispersed species on average, and one additional wind-dispersed species, in comparison with regular-mesh traps (Figure 3-4). On average, eight more tree species, six more shrub species, and three more liana species were captured in fine-mesh compared with regular-mesh traps over the course of a year (Figure 3-5).

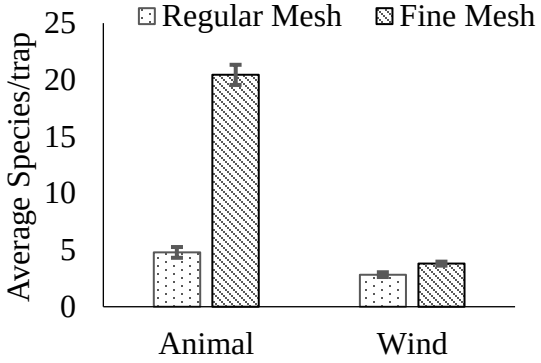

Figure 3-4. Species richness (mean annual per trap ± SE), for the most common dispersal modes.

Table 3-1. Abundance of seed rain in two mesh sizes of seed traps. Values are annual means per trap. Percentage refers to the total number of seeds captured across traps within each mesh size for each functional trait.

			Regular Mesh		*Fine Mesh*	
			Mean Trap Total ± SE	Percentage	Mean Trap Total ± SE	Percentage
Dispersal Mode		Animal	1120 ± 418	97	2116 ± 566	96
		Wind	34.6 ± 8.4	3	78 ± 17.3	3.6
		Mechanical	0	0	0.2	0.4
Life Form		Tree	476 ± 186	41	559 ± 184	27
		Shrub	646 ± 390	56	1496 ± 549	68
		Liana	31.7 ± 18.3	2.7	945 ± 18.6	4.3
		Palm	0.2	0	0.1	0
		Unknown	0.1	0	3.9	0.2
Successional Status	Liana	Generalist	29.8 ± 18.3	6.3	61.6 ± 17	20
		Secondary	1.9	0.4	33.2	11
		Old Growth	0	0	0	0
	Tree	Generalist	215 ± 124	45	219 ± 105	35
		Secondary	227 ± 151	48	320 ± 132	50
		Old-Growth	0.1	0	0.7	0.2
	Palm	Old Growth	0.2	0	0.1	0

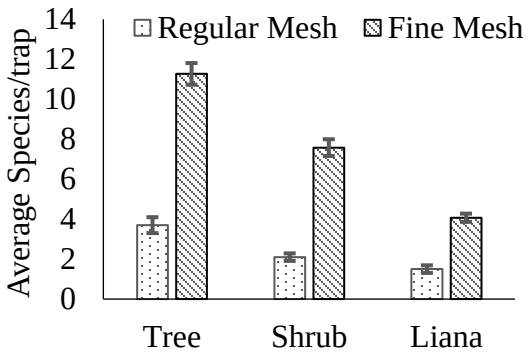

Figure 3-5. Species richness (mean annual per trap ± SE), for the most common life forms in seed rain.

Immigrating Species

Given the established understory in these experimental plots, it is possible that some species arriving in seed rain were produced from within the experimental plots. To assess the extent to which species were immigrating into the plots via seed rain, we differentiated between the species in seed rain that were already present in the understory, and those that were absent. Of the species immigrating, fine-mesh traps collected an additional 27 species of shrubs, 41 species of animal-dispersed seeds, 5 large-seeded species, and 19 species with very-small seeds, in comparison with regular-mesh traps. In the regular-mesh traps, only 18% of the species were immigrating whereas over 50% of the species in fine-mesh traps were immigrating. Of those immigrating species captured as seeds in the fine-mesh traps, 34% of the species had very-small seeds, which accounted for 70% of the total abundance of exogenous seeds in fine-mesh traps.

Interactions Between Mesh Size and Overstory Tree Species

The interaction between mesh size and overstory tree species was significant only for species richness of seed rain (mesh size * overstory tree species, $P = 0.0002$) (APPENDIX H.). Species richness was higher in fine-mesh traps for all four overstory tree species (APPENDIX H.). Species composition differed significantly between mesh sizes among the overstory tree species with Bray-Curtis and Jaccard metrics ($P = 0.001$ for both). *Virola* was the only tree species with significant differences in species composition between mesh sizes (Bray-Curtis: $P = 0.005$, and Jaccard: $P = 0.011$). This indicates that species composition of the seed rain both qualitatively and quantitatively varied between the two mesh sizes in the *Virola* plots (Table 3-2) while for the other overstory tree species plots, differences in composition between mesh sizes were not significant.

Table 3-2. Permutational Analysis of Variance (PERMANOVA) for species composition in seed rain capture in the two mesh sizes for four overstory tree species.

	Overstory tree species			
Metric	*Hieronyma*	*Virola*	*Pentaclethra*	*Vochysia*
Bray-Curtis	$P = 0.884$	$P = 0.005$*	$P = 0.792$	$P = 0.122$
Jaccard	$P = 0.713$	$P = 0.011$*	$P = 0.945$	$P = 0.258$

Discussion

Seed traps constructed with suspended mesh are a very widely used field method for quantifying seed dispersal, informing researchers about the diversity and composition of species arriving in seed rain. We found that fine-mesh traps captured a significantly greater abundance of seeds overall, higher species richness and diversity, and contained significantly different species compositions in comparison with regular-mesh traps. In this study, regular-mesh traps underestimated both species richness and abundance by 50% per trap on an annual basis compared with fine-mesh traps. The differences in species composition between the two mesh sizes varied significantly, but depended on the overstory tree species. Over 30% of the total seed rain input came from very-small seeded species, of which only 14% was captured in regular-mesh traps. Thus, the size of the mesh used to construct traps can significantly affect inferences about seed dispersal as well as the interpretation of a wide range of hypothesis tests involving data on seed rain.

Methodological Considerations

Because the fine-mesh traps captured significantly more species and different species composition than the regular-mesh traps, greater time and effort were required to sort and identify species. The fine-mesh traps captured approximately twice the abundance of seeds found in regular-mesh traps on average per trap. Fine-mesh traps also collected an additional

59 species not found in regular-mesh traps. There was no difference in time spent collecting material in the field, but the fine-mesh traps took twice the amount of time to examine material in the field than regular-mesh traps. The fine-mesh traps captured more detritus, thus increased by five-fold the time required to sort and distinguish between seeds and detritus. In the lab, it took approximately six times longer to count and identify seeds in fine-mesh than in regular-mesh traps. This research required four full-time personnel to collect, sort, germinate, if necessary, and identify species in seed rain for over 14 months.

The fine-mesh traps required additional time and effort, but the results obtained yielded different inferences about seed limitation and successional stage. More specifically, seed-rain data gathered using the regular mesh suggested greater dispersal limitation and fewer pioneer species arriving in the site. Restoration ecologists often gauge restoration success by evaluating seed limitation over time (Reid, Holl, & Zahawi 2015). Our results using only regular-mesh traps would have indicated less dominance of early-successional, animal-dispersed species. Because seed arrival sets the initial template for plant regeneration, seed rain studies can be used to inform which restoration treatment effectively allows recovery through succession (Cole, Holl, & Zawahi 2010). If 50% fewer species were captured because the mesh size was too large to capture certain very small-seeded species, one might detect fewer differences between experimental treatments. Seed traps can be used to evaluate successional changes for species arriving in the seed rain. Although not all species that arrive in the seed rain will establish and reproduce, all species which become established adults must have arrived. In this respect, seed rain provides ecological context for succession (Jesus, Pivello, Meirelles, Franco, & Metzger 2012; Wendt, 2014).

Applicability in Seed Dispersal Studies

Seed rain traps are valuable tools that can be used to quantify mechanisms limiting species diversity through the process of seed dispersal. Stevenson and Vargas (2008) determined that the mesh-lined seed trap was the most effective trap at capturing seeds and fruit in tropical rainforests, but unfortunately did not specify a mesh size. Our results show that it is important to consider mesh size within the context of the questions posed when designing and interpreting data from seed rain studies.

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CHAPTER 4. CONCLUSION

Previous studies have documented that species of overstory trees can influence seedling and sapling survival and growth differentially (Cusack and Montagnini 2004, Butler et al. 2008, Sansevero et al. 2009). The results from this research provide evidence of that tree species differ also in their filtering of seed rain. Several attributes of the four experimental tree species were significantly correlated with seed rain including species richness and composition. Thus, these results demonstrated that individual tree species can play a role in shaping their local plant communities via effects on arrival of seeds to tropical forests, especially for species dispersed by animals. This research also documented the differences in seed capture due to mesh size used in seed traps.

Chapter 2 described our finding that overstory tree species differed significantly in their effects on seed rain, specifically its species richness and composition. Seed rain under *Pentaclethra macroloba*, contained significantly fewer species of trees and lianas that were animal-dispersed compared with the three other overstory tree species. *Pentaclethra*, a mechanically dispersed, nitrogen-fixing legume, is the dominant tree species at La Selva. Consistent with other studies, overstory tree species that provided food resources that attract animal dispersers, contained the greatest species diversity in the seed rain (Slocum 2001, Trolliet et al. 2017). Contrary to neutral theory that predicts that seed arrival is random (Lowe and McPeek 2014), we found evidence of deterministic seed arrival for both wind- and animal-dispersed species. The results from this thesis have implications for restoration projects in which regeneration of species diversity is a goal, particularly in the tropical rainforest. Additionally, these results imply that dispersal kernels may not have a smooth decline with distance from the parent plant (Morales and Carlo 2006). Our results suggest

that in the tropics, fruiting trees may attract animals and thereby add additional smaller peaks of seed rain to specific tree species.

In Chapter 3, we evaluated the effect of mesh size on seed capture in seed traps by examining differences between two mesh sizes. We found significant differences between the two mesh sizes in the abundance, species richness, species diversity and composition of seed rain captured. As predicted fewer of the very-small seeded species, 19 out of 21, were not captured in the most commonly used 1-mm mesh seed traps. These results provide evidence that results, and implications drawn from those results will differ significantly depending on mesh size. Additionally, we found that the effects of mesh size on seed rain differed significantly among the four overstory tree species suggesting that not all study sites require a fine mesh for capturing an unbiased sample of the seed rain.

Overall the results obtained suggested that overstory tree species differ in their role in filtering the pool of species that is available for regeneration within a neighborhood. By using a fine-mesh fabric liner (Terylene®, 1 μm) in the seed traps, we captured very small-sized seeds that are generally missed in most studies of tropical seed rain. The fine-mesh traps were quite labor-intensive, requiring up to five times longer to process the larger seed samples that were more difficult to identify to species. Thus, there is inherent trade-off between time and effort expended and capture of very small-seeds.

Future Directions and Closing Remarks

This thesis provides insight into the extent to which overstory tree species differ in their effects on regeneration in the surrounding local plant neighborhood. Because overstory trees differ in their effects on species composition at this first stage of dispersal, there will be subsequent effects within the local neighborhood for future processes, including competition

and density-dependent survival of seedlings. In completing this work, there are several potential avenues for future research that can increase our understanding of the role of diversity maintenance. These include comparison of seed rain composition of seedling and adult composition within plots, phenology of seed rain, succession of woody species within these plots and surveys for animal disperser presence and activity within plots.

These plots had already been regenerating for over 25 years when this study was conducted. Nevertheless, half of the species in the seed rain captured did not already occur in the plots and were thus immigrating. This suggests that the differences in effects of overstory tree species on regeneration continues to affect seed arrival (dispersal limitation) and thus could also continue to filter species through establishment limitation. Previous studies on woody regeneration conducted in these same experimental plots provided a basis for comparison with our study. At year 7, species richness of naturally occurring woody regeneration was higher under *Pentaclethra* and *Vochysia,* the abiotically dispersed tree species. These two species contained 22 more understory species than the animal-dispersed overstory tree species (Powers et al. 1997). Powers et al. (1997) concluded that facilitation of woody regeneration in *Hieronyma* and *Virola* (animal-dispersed species) was no different than in the unplanted control; thus, seed dispersal did not play a critical role in structuring the communities. Nearly 20 years later, we found that species richness was higher in *Hieronyma*, and *Virola* than *Pentaclethra.* Although the differences in diversity in the two studies at this site, (seed rain vs seedling establishment) are not directly comparable, they suggest that overstory tree species differ in their effects on woody regeneration over the course of succession. It is possible these differences are due to the stage of reproduction of the overstory tree species, and their concomitant attractiveness for animal dispersers. *Hieronyma*

reaches reproductive maturity at approximately 10 years, *Virola* at ~12 years. Thus, neither of these animal-dispersed overstory tree species had been providing fruit as a food resources for animals at Year 7. Comparing data on woody regeneration during the years that seed rain were collected could help explain differences observed over time within these plots, as well as the relative importance of seed limitation and establishment limitation by comparing seed to seedling transitions (Muscarella et al. 2013).

Furthermore, our results show differences in animal-dispersed species found in seed rain, but we know nothing about what the identify of the animal dispersers that produce this variation. Future studies can examine disperser use, diversity and behavior within each overstory tree species plot to identify specific mechanisms and traits that would influence plant species diversity. Other studies that would prove interesting include phenological comparisons that examine spatial variation over time across species of different dispersal modes in seed rain.

Future studies should also consider number of seed-rain traps required to sample arriving species diversity and richness (Kollmann and Goetze 1998). It is possible that our experimental design under-sampled the diversity at La Selva given the approximately 1000 woody species which occur there. However, our results provide support that plant species diversity in seed rain will be measured more fully by using a fine mesh, given the number of very-small-seeded species at this site.

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APPENDIX A. ECOLOGICAL TRAITS OF SPECIES IN SEED RAIN

Species trait data were collected from the La Selva and other literature. Species life form was determined using Tropicos (http://tropicos.org/), a plant specimen database specific to the tropics, La Selva Florula Digital, and with help from Dr. Susan Letcher. Species dispersal mode was determined using La Selva Florula Digital, Vargas (2000) and with help from Dr. Susan Letcher. Sources for seed size included Vargas (2000), data from this study (ECOS), Letcher (2008), Wendt (2014), as specified (Table A-1). Successional stage for tree species followed Chazdon et al. (2011); however, to generalize terms across life forms, 'old-growth specialists' as determined by Chazdon were denoted as 'old growth', and 'secondary-specialists' were denoted as 'secondary.' Successional stage for liana species followed Letcher (2008); however, to generalize terms across life forms, 'young forest' liana species were categorized as 'secondary', and similarly rather than 'old forest', we used 'old growth'.

Table A-1. Life form, dispersal mode, seed size and successional status of seed-rain species.

Species	Life Form	Dispersal Mode	Seed Size	Seed size source	Successional Status
Adelobotrys adscendens	Liana	Animal	Small	Vargas	Generalist
Alchorneopsis floribunda	Tree	Animal	Small	ECOS	Generalist
Annona papilionella	Tree	Animal	Medium	ECOS	Secondary
Apeiba membranacea	Tree	Mechanical	Small	ECOS	Generalist
Aristolochia sprucei	Liana	Wind	Small	ECOS	Secondary
Asterogyne martiana	Palm	Animal	Medium	ECOS	Old growth
Bertiera guianensis	Shrub	Animal	Small	ECOS	
Bignonia binata	Liana	Wind	Medium	Vargas	Generalist
Brosimum lactescens	Tree	Animal	Medium	Wendt	Old growth
Bursera simaruba	Tree	Animal	Medium	Vargas	
Byrsonima crassifolia	Tree	Animal	Medium	Wendt	Secondary
Casearia arborea	Tree	Animal	Small	ECOS	Secondary
Cecropia insignis	Tree	Animal	Small	ECOS	Secondary

Table A-1. (continued)

Species	**Life Form**	**Dispersal Mode**	**Seed Size**	**Seed size source**	**Successional Status**
Cecropia obtusifolia	Tree	Animal	Small	ECOS	Generalist
Cespedesia spathulata	Tree	Wind	Small	Wendt	Generalist
Cestrum schlechtendalii	Shrub	Animal	Medium	Vargas	
Clethra sp	Tree	Animal	Small	Vargas	
Clidemia crenulata	Shrub	Animal	Small	ECOS	
Clidemia densiflora	Shrub	Animal	Small	ECOS	
Clidemia dentata	Shrub	Animal	Small	ECOS	
Clidemia discolor	Shrub	Animal	Small	ECOS	
Clidemia japurensis	Shrub	Animal	Small	ECOS	
Conostegia subcrustulata	Shrub	Animal	Small	ECOS	
Conostegia xalapensis	Shrub	Animal	Small	Vargas	
Cordia alliodora	Tree	Wind	Medium	ECOS	Secondary
Cordia bicolor	Tree	Animal	Medium	ECOS	Secondary
Davilla nitida	Liana	Animal	Small	ECOS	Secondary
Dendropanax arboreus	Tree	Animal	Small	ECOS	Old growth
Doliocarpus multiflorus	Liana	Animal	Medium	ECOS	Generalist
Euterpe precatoria	Palm	Animal	Medium	ECOS	Old growth
Ficus colubrinae	Tree	Animal	Small	Wendt	
Ficus donnell-smithii	Shrub	Animal	Small	Vargas	
Ficus insipida	Tree	Animal	Small	ECOS	
Ficus nymphaefolia	Tree	Animal	Small	ECOS	
Ficus pertusa	Shrub	Animal	Small	ECOS	
Ficus sp	NA	Animal	Small	Vargas	
Ficus sp2	NA	Animal	Small	Vargas	
Forsteronia myriantha	Liana	Wind	Small	Letcher	Generalist
Goethalsia meiantha	Tree	Wind	Small	ECOS	Secondary
Gouania polygama	Liana	Wind	Small	ECOS	Generalist
Guatteria aeruginosa	Tree	Animal	Medium	ECOS	Old growth
Guatteria amplifolia	Tree	Animal	Medium	ECOS	Secondary
Guatteria recurvisepala	Tree	Animal	Medium	ECOS	
Hamelia xerocarpa	Shrub	Animal	Small	Vargas	
Hampea appendiculata	Tree	Animal	Medium	ECOS	Secondary
Heisteria scandens	Liana	Animal	Medium	Vargas	Old growth
Hieronyma alchorneoides	Tree	Animal	Small	ECOS	Generalist
Iriartea deltoidea	Palm	Animal	Large	ECOS	Old growth

Table A-1. (continued)

Species	**Life Form**	**Dispersal Mode**	**Seed Size**	**Seed size source**	**Successional Status**
Jacaranda copaia	Tree	Wind	Small	Wendt	Secondary
Laetia procera	Tree	Animal	Small	ECOS	Secondary
Lauraceae	NA	Animal	Large	Vargas	
Leandra granatensis	Tree	Animal	Small	ECOS	
Leandra longicoma	Shrub	Animal	Small	ECOS	
Luehea seemannii	Tree	Wind	Small	ECOS	Generalist
Mandevilla hirsuta	Liana	Wind	Medium	ECOS	Generalist
Mendoncia tonduzii	Liana	Animal	Medium	Florula digital	Generalist
Miconia affinis	Shrub	Animal	Small	Vargas	Secondary
Miconia approximata	Shrub	Animal	Small	Vargas	
Miconia elata	Tree	Animal	Small	ECOS	Secondary
Miconia lacera	Shrub	Animal	Small	ECOS	
Miconia ligulata	Shrub	Animal	Small	Vargas	
Miconia multispicata	Tree	Animal	Small	ECOS	Secondary
Miconia nervosa	Shrub	Animal	Small	Vargas	
Miconia prasina	Shrub	Animal	Small	Wendt	
Miconia stevensiana	Tree	Animal	Small	Wendt	
Myrcia splendens	Shrub	Animal	Medium	ECOS	
Nectandra membranacea	Tree	Animal	Medium	ECOS	
Neea laetevirens	Tree	Animal	Small	ECOS	Secondary
Palicourea guianensis	Shrub	Animal	Small	ECOS	
Paullinia fasciculata	Liana	Animal	Large	Letcher	Generalist
Paullinia granatensis	Liana	Animal	Large	Letcher	Old growth
Paullinia ingifolia	Liana	Animal	Large	Letcher	Old growth
Piper aduncum	Shrub	Animal	Small	ECOS	
Piper auritifolium	Shrub	Animal	Small	Vargas	
Piper auritum	Shrub	Animal	Small	ECOS	
Piper colonense	Shrub	Animal	Small	ECOS	
Piper melanocladum	Shrub	Animal	Small	Vargas	
Piper multiplinervium	Liana	Animal	Small	ECOS	Old growth
Piper peltatum	Shrub	Animal	Small	ECOS	
Piper sancti-felicis	Shrub	Animal	Small	ECOS	
Piper schiedeanum	Shrub	Animal	Small	Vargas	
Piper sp	Shrub	Animal	Small	Vargas	

Table A-1. (continued)

Species	**Life Form**	**Dispersal Mode**	**Seed Size**	**Seed size source**	**Successional Status**
Piper trigonum	Shrub	Animal	Small	ECOS	
Piptocarpha poeppigiana	Shrub	Wind	Small	ECOS	
Prestoea decurrens	Palm	Animal	Medium	Vargas	Old growth
Protium sp	Tree	Animal	Large	Vargas	
Psychotria brachiata	Shrub	Animal	Small	ECOS	
Psychotria chiapensis	Shrub	Animal	Medium	ECOS	
Psychotria gracilenta	Shrub	Animal	Small	ECOS	
Psychotria luxurians	Tree	Animal	Small	ECOS	
Psychotria marginata	Shrub	Animal	Small	ECOS	
Psychotria panamensis	Tree	Animal	Medium	Wendt	Old growth
Psychotria poeppigiana	Shrub	Animal	Medium	ECOS	
Psychotria sp	Shrub	Animal	Small	Vargas	
Rubiaceae	NA	Animal	Small	Vargas	
Sabicea panamensis	Liana	Animal	Medium	Florula digital	Generalist
Sabicea villosa	Liana	Animal	Medium	Florula digital	Generalist
Schefflera nicaraguensis	Shrub	Animal	Medium	Vargas	
Schlegelia fastigiata	Liana	Animal	Large	Letcher	Generalist
Senna papillosa	Tree	Animal	Small	ECOS	
Serjania mexicana	Liana	Wind	Medium	Letcher	Generalist
Serjania pyramidata	Liana	Wind	Medium	Vargas	Generalist
Simarouba amara	Tree	Animal	Medium	ECOS	Secondary
Siparuna grandiflora	Shrub	Animal	Small	ECOS	
Siparuna pauciflora	Shrub	Animal	Medium	ECOS	
Siparuna thecaphora	Shrub	Animal	Small	ECOS	
Smilax officinalis	Liana	Animal	Medium	Vargas	Generalist
Solanum rugosum	Shrub	Animal	Small	Vargas	
Talauma gloriensis	Tree	Animal	Medium	Wendt	
Tetrapterys sp	Liana	Wind	Large	Vargas	Generalist
Urera caracasana	Shrub	Animal	Small	Vargas	
Virola koschnyi	Tree	Animal	Large	ECOS	Generalist
Virola sebifera	Tree	Animal	Medium	ECOS	Generalist
Vismia baccifera	Tree	Animal	Small	ECOS	Secondary
Vismia billbergiana	Tree	Animal	Small	ECOS	
Vismia macrophylla	Tree	Animal	Small	ECOS	

Table A-1. (continued)

Species	**Life Form**	**Dispersal Mode**	**Seed Size**	**Seed size source**	**Successional Status**
Vochysia ferruginea	Tree	Wind	Medium	ECOS	Secondary
Vochysia guatemalensis	Tree	Wind	Large	ECOS	Secondary
Warszewiczia coccinea	Tree	Wind	Small	ECOS	Old growth
Xylopia sericophylla	Tree	Animal	Medium	ECOS	Secondary
Zanthoxylum panamense	Tree	Animal	Small	Wendt	Secondary

APPENDIX B. ANNUAL SEED RAIN IN FOUR OVERSTORY TREE SPECIES

Table B-1. Annual seed rain abundance and density by species across four overstory tree species.

		Hieronyma alchorneoides			***Virola koschnyi***			***Pentaclethra macroloba***			***Vochysia guatemalensis***			**Total**	
Family	**Species and Authority**	Abund.	Density	%	Abund.	Density	%	Abund.	Density	%	Abund.	Density	%	Abund	%
Melastomataceae	*Adelobotrys adscendens* (Sw.) Triana	0	0.00	0%	0	0.0	0%	0	0.0	0%	139	17.8	100 %	139	0%
Euphorbiaceae	*Alchorneopsis floribunda* (Benth.) Müll. Arg.	612	58.85	5%	1697	163.2	13%	10780	1036.5	81%	267	34.2	2%	13356	10%
Annonaceae	*Annona papilionella* (Diels) H. Rainer	11	1.06	52%	5	0.5	24%	1	0.1	5%	4	0.5	19%	21	0%
Malvaceae	*Apeiba membranacea* Spruce ex Benth.	2	0.19	29%	0	0.0	0%	0	0.0	0%	5	0.6	71%	7	0%
Aristolochiaceae	*Aristolochia sprucei* Mast.	s	0.10	3%	18	1.7	47%	7	0.7	18%	12	1.5	32%	38	0%
Arecaceae	*Asterogyne martiana* (H. Wendl.) H. Wendl. ex Hemsl.	0	0.00	0%	1	0.1	33%	2	0.2	67%	0	0.0	0%	3	0%
Rubiaceae	*Bertiera guianensis* Aubl.	41	3.94	100 %	0	0.0	0%	0	0.0	0%	0	0.0	0%	41	0%
Bignoniaceae	*Bignonia binata* Thunb.	0	0.00	0%	0	0.0	0%	1	0.1	100 %	0	0.0	0%	1	0%
Moraceae	*Brosimum lactescens* (S. Moore) C.C. Berg	0	0.00	0%	4	0.4	100 %	0	0.0	0%	0	0.0	0%	4	0%
Burseraceae	*Bursera simaruba* (L.) Sarg.	0	0.00	0%	0	0.0	0%	0	0.0	0%	1	0.1	100 %	1	0%
Malpighiaceae	*Byrsonima crassifolia* (L.) Kunth	8	0.77	89%	1	0.1	11%	0	0.0	0%	0	0.0	0%	9	0%
Salicaceae	*Casearia arborea* (Rich.) Urb.	5	0.48	9%	50	4.8	88%	0	0.0	0%	2	0.3	4%	57	0%
Urticaceae	*Cecropia insignis* Liebm.	117	11.25	33%	87	8.4	24%	71	6.8	20%	81	10.4	23%	356	0%
Urticaceae	*Cecropia obtusifolia* Bertol.	802	77.12	29%	1154	111.0	41%	129	12.4	5%	708	90.8	25%	2793	2%
Ochnaceae	*Cespedesia spathulata* (Ruiz & Pav.) Planch.	2	0.19	50%	1	0.1	25%	1	0.1	25%	0	0.0	0%	4	0%
Solanaceae	*Cestrum schlechtendalii* G. Don	3	0.29	75%	0	0.0	0%	1	0.1	25%	0	0.0	0%	4	0%
Clethraceae	*Clethra sp*	0	0.00	0%	0	0.0	0%	1	0.1	100 %	0	0.0	0%	1	0%
Melastomataceae	*Clidemia crenulata* Gleason	3	0.29	0%	34	3.3	5%	624	60.0	94%	0	0.0	0%	661	0%

Table B-1. (continued)

		Hieronyma alchorneoides			***Virola koschnyi***			***Pentaclethra macroloba***			***Vochysia guatemalensis***			**Total**	
Family	**Species and Authority**	Abund.	Density	%	Abund.	Density	%	Abund.	Density	%	Abund.	Density	%	Abund	%
Melastomataceae	*Clidemia densiflora* (Standl.) Gleason	19	1.83	95%	1	0.1	5%	0	0.0	0%	0	0.0	0%	20	0%
Melastomataceae	*Clidemia dentata* Pav. ex D. Don	5	0.48	3%	79	7.6	41%	3	0.3	2%	105	13.5	55%	192	0%
Melastomataceae	*Clidemia discolor* (Triana) Cogn.	4	0.38	100 %	0	0.0	0%	0	0.0	0%	0	0.0	0%	4	0%
Melastomataceae	*Clidemia japurensis* DC.	24	2.31	1%	2401	230.9	84%	187	18.0	7%	236	30.3	8%	2848	2%
Melastomataceae	*Conostegia subcrustulata* (Beurl.) Triana	0	0.00	0%	1	0.1	100 %	0	0.0	0%	0	0.0	0%	1	0%
Melastomataceae	*Conostegia xalapensis* (Bonpl.) D. Don ex DC.	2	0.19	100 %	0	0.0	0%	0	0.0	0%	0	0.0	0%	2	0%
Boraginaceae	*Cordia alliodora* (Ruiz & Pav.) Oken	2	0.19	5%	4	0.4	10%	30	2.9	73%	5	0.6	12%	41	0%
Boraginaceae	*Cordia bicolor* A. DC.	0	0.00	0%	1	0.1	14%	6	0.6	86%	0	0.0	0%	7	0%
Dilleniaceae	*Davilla nitida* (Vahl) Kubitzki	140	13.46	89%	6	0.6	4%	5	0.5	3%	6	0.8	4%	157	0%
Araliaceae	*Dendropanax arboreus* (L.) Decne. & Planch	0	0.00	0%	1	0.1	100 %	0	0.0	0%	0	0.0	0%	1	0%
Dilleniaceae	*Doliocarpus multiflorus* Standl.	8	0.77	11%	5	0.5	7%	60	5.8	82%	0	0.0	0%	73	0%
Arecaceae	*Euterpe precatoria* Mart.	0	0.00	0%	0	0.0	0%	4	0.4	80%	1	0.1	20%	5	0%
Moraceae	*Ficus colubrinae* Standl.	16	1.54	53%	4	0.4	13%	3	0.3	10%	7	0.9	23%	30	0%
Moraceae	*Ficus donnell-smithii* Standl.	4	0.38	100 %	0	0.0	0%	0	0.0	0%	0	0.0	0%	4	0%
Moraceae	*Ficus insipida* Willd.	779	74.90	68%	294	28.3	26%	49	4.7	4%	17	2.2	1%	1139	1%
Moraceae	*Ficus nymphaefolia* Mill.	158	15.19	69%	1	0.1	0%	0	0.0	0%	70	9.0	31%	229	0%
Moraceae	*Ficus pertusa* L. f.	1	0.10	20%	2	0.2	40%	0	0.0	0%	2	0.3	40%	5	0%
Moraceae	*Ficus sp*	31	2.98	35%	22	2.1	25%	2	0.2	2%	33	4.2	38%	88	0%
Moraceae	*Ficus sp2*	0	0.00	0%	3	0.3	60%	2	0.2	40%	0	0.0	0%	5	0%
Apocynaceae	*Forsteronia myriantha* Donn. Sm.	0	0.00	0%	1	0.1	100 %	0	0.0	0%	0	0.0	0%	1	0%
Malvaceae	*Goethalsia meiantha* (Donn. Sm.) Burret	0	0.00	0%	0	0.0	0%	0	0.0	0%	2	0.3	100 %	2	0%

Table B-1. (continued)

		Hieronyma alchorneoides			***Virola koschnyi***			***Pentaclethra macroloba***			***Vochysia guatemalensis***			**Total**	
Family	**Species and Authority**	Abund.	Density	%	Abund.	Density	%	Abund.	Density	%	Abund.	Density	%	Abund	%
Rhamnaceae	*Gouania polygama* (Jacq.) Urb.	13	1.25	4%	10	1.0	3%	275	26.4	91%	4	0.5	1%	302	0%
Annonaceae	*Guatteria aeruginosa* Standl.	2	0.19	100%	0	0.0	0%	0	0.0	0%	0	0.0	0%	2	0%
Annonaceae	*Guatteria amplifolia* Triana & Planch.	1	0.10	13%	0	0.0	0%	1	0.1	13%	6	0.8	75%	8	0%
Annonaceae	*Guatteria recurvisepala* R.E. Fr.	172	16.54	75%	6	0.6	3%	45	4.3	20%	7	0.9	3%	230	0%
Rubiaceae	*Hamelia xerocarpa* Kuntze	2	0.19	100%	0	0.0	0%	0	0.0	0%	0	0.0	0%	2	0%
Malvaceae	*Hampea appendiculata* (Donn. Sm.) Standl.	5	0.48	83%	0	0.0	0%	0	0.0	0%	1	0.1	17%	6	0%
Erythropalaceae	*Heisteria scandens* Ducke	0	0.00	0%	0	0.0	0%	0	0.0	0%	1	0.1	100%	1	0%
Phyllanthaceae	*Hieronyma alchorneoides* Allemão	0	0.00	0%	15	1.4	25%	36	3.5	59%	10	1.3	16%	61	0%
Arecaceae	*Iriartea deltoidea* Ruiz & Pav.	1	0.10	100%	0	0.0	0%	0	0.0	0%	0	0.0	0%	1	0%
Bignoniaceae	*Jacaranda copaia* (Aubl.) D. Don	2	0.19	14%	2	0.2	14%	7	0.7	50%	3	0.4	21%	14	0%
Salicaceae	*Laetia procera* (Poepp.) Eichler	45	4.33	92%	3	0.3	6%	0	0.0	0%	1	0.1	2%	49	0%
Lauraceae	*Lauraceae*	0	0.00	0%	0	0.0	0%	1	0.1	100%	0	0.0	0%	1	0%
Melastomataceae	*Leandra granatensis* Gleason	26	2.50	2%	69	6.6	6%	1026	98.7	91%	9	1.2	1%	1130	1%
Melastomataceae	*Leandra longicoma* Cogn.	1	0.10	11%	5	0.5	56%	2	0.2	22%	1	0.1	11%	9	0%
Malvales	*Luehea seemannii* Triana & Planch.	9	0.87	15%	15	1.4	24%	36	3.5	58%	2	0.3	3%	62	0%
Apocynaceae	*Mandevilla hirsuta* (Rich.) K. Schum.	5	0.48	8%	32	3.1	51%	1	0.1	2%	25	3.2	40%	63	0%
Acanthaceae	*Mendoncia tonduzii* Turrill	0	0.00	0%	1	0.1	100%	0	0.0	0%	0	0.0	0%	1	0%
Melastomataceae	*Miconia affinis* DC.	33008	3173.85	90%	1332	128.1	4%	1889	181.6	5%	413	52.9	1%	36642	27%
Melastomataceae	*Miconia approximata* Gamba & Almeda	6	0.58	100%	0	0.0	0%	0	0.0	0%	0	0.0	0%	6	0%
Melastomataceae	*Miconia elata* (Sw.) *DC.*	71	6.83	41%	52	5.0	30%	21	2.0	12%	28	3.6	16%	172	0%
Melastomataceae	*Miconia lacera* (Bonpl.) Naudin	9	0.87	4%	9	0.9	4%	16	1.5	7%	203	26.0	86%	237	0%

Table B-1. (continued)

		Hieronyma alchorneoides			***Virola koschnyi***			***Pentaclethra macroloba***			***Vochysia guatemalensis***			**Total**	
Family	**Species and Authority**	Abund.	Density	%	Abund.	Density	%	Abund.	Density	%	Abund.	Density	%	Abund	%
Melastomataceae	*Miconia ligulata* Almeda	23	2.21	27%	58	5.6	67%	5	0.5	6%	0	0.0	0%	86	0%
Melastomataceae	*Miconia multispicata* Naudin	6000	576.92	31%	11380	1094.2	58%	1518	146.0	8%	666	85.4	3%	19564	15%
Melastomataceae	*Miconia nervosa* (Sm.) Triana	0	0.00	0%	1	0.1	100 %	0	0.0	0%	0	0.0	0%	1	0%
Melastomataceae	*Miconia prasina* (Sw.) DC.	2	0.19	100 %	0	0.0	0%	0	0.0	0%	0	0.0	0%	2	0%
Melastomataceae	*Miconia stevensiana* Almeda	1	0.10	100 %	0	0.0	0%	0	0.0	0%	0	0.0	0%	1	0%
Myrtaceae	*Myrcia splendens* (Sw.) DC.	723	69.52	80%	4	0.4	0%	165	15.9	18%	17	2.2	2%	909	1%
Lauraceae	*Nectandra membranacea* (Sw.) Griseb.	3	0.29	50%	0	0.0	0%	1	0.1	17%	2	0.3	33%	6	0%
Nyctaginaceae	*Neea laetevirens* Standl.	31	2.98	91%	1	0.1	3%	2	0.2	6%	0	0.0	0%	34	0%
Rubiaceae	*Palicourea guianensis* Aubl.	0	0.00	0%	0	0.0	0%	0	0.0	0%	1	0.1	100 %	1	0%
Sapindaceae	*Paullinia fasciculata* Radlk.	0	0.00	0%	2	0.2	100 %	0	0.0	0%	0	0.0	0%	2	0%
Sapindaceae	*Paullinia granatensis* (Planch. & Linden) Radlk	0	0.00	0%	0	0.0	0%	0	0.0	0%	1	0.1	100 %	1	0%
Sapindaceae	*Paullinia ingifolia* Rich. ex Juss	0	0.00	0%	0	0.0	0%	0	0.0	0%	1	0.1	100 %	1	0%
Piperaceae	*Piper aduncum* L.	7	0.67	6%	88	8.5	73%	21	2.0	17%	5	0.6	4%	121	0%
Piperaceae	*Piper auritifolium* Trel	0	0.00	0%	0	0.0	0%	11550	1110.6	100 %	0	0.0	0%	11550	9%
Piperaceae	*Piper auritum* Kunth	112	10.77	34%	80	7.7	25%	20	1.9	6%	113	14.5	35%	325	0%
Piperaceae	*Piper colonense* C. DC.	5899	567.21	20%	13986	1344.8	48%	6799	653.8	23%	2385	305.8	8%	29069	22%
Piperaceae	*Piper melanocladum* C. DC.	0	0.00	0%	2	0.2	100 %	0	0.0	0%	0	0.0	0%	2	0%
Piperaceae	*Piper multiplinervium* C. DC.	505	48.56	37%	345	33.2	25%	193	18.6	14%	313	40.1	23%	1356	1%
Piperaceae	*Piper peltatum* L.	0	0.00	0%	65	6.3	100 %	0	0.0	0%	0	0.0	0%	65	0%
Piperaceae	*Piper sancti-felicis* Trel.	25	2.40	30%	34	3.3	41%	4	0.4	5%	19	2.4	23%	82	0%
Piperaceae	*Piper schiedeanum* Steud.	0	0.00	0%	1	0.1	50%	0	0.0	0%	1	0.1	50%	2	0%
Piperaceae	*Piper sp*	36	3.46	47%	23	2.2	30%	3	0.3	4%	14	1.8	18%	76	0%

Table B-1. (continued)

		Hieronyma alchorneoides			*Virola koschnyi*			*Pentaclethra macroloba*			*Vochysia guatemalensis*			**Total**	
Family	**Species and Authority**	Abund.	Density	%	Abund.	Density	%	Abund.	Density	%	Abund.	Density	%	Abund	%
Piperaceae	*Piper trigonum* C. DC.	14	1.35	50%	9	0.9	32%	3	0.3	11%	2	0.3	7%	28	0%
Asteraceae	*Piptocarpha poeppigiana* (DC.) Baker	731	70.29	20%	1974	189.8	55%	449	43.2	13%	438	56.2	12%	3592	3%
Arecaceae	*Prestoea decurrens* (H. Wendl. ex Burret) H.E. Moore	0	0.00	0%	0	0.0	0%	0	0.0	0%	1	0.1	100 %	1	0%
Burseraceae	*Protium sp*	1	0.10	100 %	0	0.0	0%	0	0.0	0%	0	0.0	0%	1	0%
Rubiaceae	*Psychotria brachiata* Sw.	2	0.19	20%	0	0.0	0%	0	0.0	0%	8	1.0	80%	10	0%
Rubiaceae	*Psychotria chiapensis* Standl.	0	0.00	0%	14	1.3	93%	1	0.1	7%	0	0.0	0%	15	0%
Rubiaceae	*Psychotria gracilenta* Müll. Arg.	3	0.29	17%	1	0.1	6%	11	1.1	61%	3	0.4	17%	18	0%
Rubiaceae	*Psychotria luxurians* Rusby	0	0.00	0%	2	0.2	100 %	0	0.0	0%	0	0.0	0%	2	0%
Rubiaceae	*Psychotria marginata* Sw.	1	0.10	10%	0	0.0	0%	1	0.1	10%	8	1.0	80%	10	0%
Rubiaceae	*Psychotria panamensis* Standl.	1	0.10	33%	2	0.2	67%	0	0.0	0%	0	0.0	0%	3	0%
Rubiaceae	*Psychotria poeppigiana* Müll. Arg.	0	0.00	0%	0	0.0	0%	5	0.5	100 %	0	0.0	0%	5	0%
Rubiaceae	*Psychotria sp*	2	0.19	100 %	0	0.0	0%	0	0.0	0%	0	0.0	0%	2	0%
Rubiaceae	*Rubiaceae*	18	1.73	22%	35	3.4	43%	11	1.1	13%	18	2.3	22%	82	0%
Rubiaceae	*Sabicea panamensis* Wernham	296	28.46	84%	18	1.7	5%	1	0.1	0%	36	4.6	10%	351	0%
Rubiaceae	*Sabicea villosa* Schult.	1488	143.08	56%	441	42.4	17%	281	27.0	11%	435	55.8	16%	2645	2%
Araliaceae	*Schefflera nicaraguensis* (Standl.) A.C. Sm.	1	0.10	100 %	0	0.0	0%	0	0.0	0%	0	0.0	0%	1	0%
Schlegeliaceae	*Schlegelia fastigiata* Schery	0	0.00	0%	1	0.1	33%	0	0.0	0%	2	0.3	67%	3	0%
Fabaceae	*Senna papillosa* (Britton & Rose) H.S. Irwin & Barneby	0	0.00	0%	1	0.1	100 %	0	0.0	0%	0	0.0	0%	1	0%
Sapindaceae	*Serjania mexicana* (L.) Willd.	1	0.10	100 %	0	0.0	0%	0	0.0	0%	0	0.0	0%	1	0%
Sapindaceae	*Serjania pyramidata* Radlk.	4	0.38	5%	70	6.7	90%	2	0.2	3%	2	0.3	3%	78	0%
Simaroubaceae	*Simarouba amara* Aubl.	118	11.35	94%	0	0.0	0%	5	0.5	4%	2	0.3	2%	125	0%
Siparunaceae	*Siparuna grandiflora* (Kunth) Perkins	0	0.00	0%	1	0.1	100 %	0	0.0	0%	0	0.0	0%	1	0%

Table B-1. (continued)

		Hieronyma alchorneoides			***Virola koschnyi***			***Pentaclethra macroloba***			***Vochysia guatemalensis***			**Total**	
Family	**Species and Authority**	Abund.	Density	%	Abund.	Density	%	Abund.	Density	%	Abund.	Density	%	Abund	%
Siparunaceae	*Siparuna pauciflora* (Beurl.) A. DC.	0	0.00	0%	1	0.1	100 %	0	0.0	0%	0	0.0	0%	1	0%
Siparunaceae	*Siparuna thecaphora* (Poepp. & Endl.) A. DC.	0	0.00	0%	1	0.1	100 %	0	0.0	0%	0	0.0	0%	1	0%
Smilacaceae	*Smilax officinalis* Kunth	0	0.00	0%	0	0.0	0%	1	0.1	100 %	0	0.0	0%	1	0%
Solanaceae	*Solanum rugosum* Dunal	10	0.96	37%	11	1.1	41%	0	0.0	0%	6	0.8	22%	27	0%
Magnoliaceae	*Talauma gloriensis* Pittier	0	0.00	0%	0	0.0	0%	0	0.0	0%	2	0.3	100 %	2	0%
Malpighiaceae	*Tetrapterys sp*	0	0.00	0%	0	0.0	0%	0	0.0	0%	7	0.9	100 %	7	0%
Urticaceae	*Urera caracasana* (Jacq.) Gaudich. ex Griseb	0	0.00	0%	0	0.0	0%	1	0.1	20%	4	0.5	80%	5	0%
Myristicaceae	*Virola koschnyi* Warb.	1	0.10	33%	0	0.0	0%	1	0.1	33%	1	0.1	33%	3	0%
Myristicaceae	*Virola sebifera* Aubl.	11	1.06	58%	3	0.3	16%	1	0.1	5%	4	0.5	21%	19	0%
Hypericaceae	*Vismia baccifera* (L.) Triana & Planch.	25	2.40	9%	66	6.3	24%	5	0.5	2%	180	23.1	65%	276	0%
Hypericaceae	*Vismia billbergiana* Beurl.	53	5.10	11%	382	36.7	79%	1	0.1	0%	48	6.2	10%	484	0%
Hypericaceae	*Vismia macrophylla* Kunth	205	19.71	47%	37	3.6	9%	43	4.1	10%	148	19.0	34%	433	0%
Vochysiaceae	*Vochysia ferruginea* Mart.	140	13.46	45%	11	1.1	4%	141	13.6	45%	21	2.7	7%	313	0%
Vochysiaceae	*Vochysia guatemalensis* Donn. Sm.	1	0.10	17%	5	0.5	83%	0	0.0	0%	0	0.0	0%	6	0%
Rubiaceae	*Warszewiczia coccinea* (Vahl) Klotzsch	1	0.10	4%	0	0.0	0%	22	2.1	96%	0	0.0	0%	23	0%
Annonaceae	*Xylopia sericophylla* Standl. & L.O. Williams	134	12.88	82%	4	0.4	2%	12	1.2	7%	14	1.8	9%	164	0%
Rutaceae	*Zanthoxylum panamense* P. Wilson	2	0.19	20%	6	0.6	60%	0	0.0	0%	2	0.3	20%	10	0%

APPENDIX C. SEED RAIN SPATIAL VARIATION IN ABUNDANCE, SPECIES RICHNESS AND DIVERSITY AMONG FOUR TREE SPECIES

We used variograms of model residuals and bubbleplots to determine if spatial autocorrelation existed. Variograms provide visualizations of spatial autocorrelation at the scale of the study. With bubbleplots, similar size and color indicate clustering of data points and possible spatial autocorrelation. We found no spatial correlation in three responses used in our models: total seed abundance, species richness and Shannon-Weiner diversity. Therefore, spatial variation was not included in our models. The figures are provided below for abundance (Figure C-1, Figure C-2), species richness (Figure C-3, Figure C-4), and diversity (Figure C-5, Figure C-6).

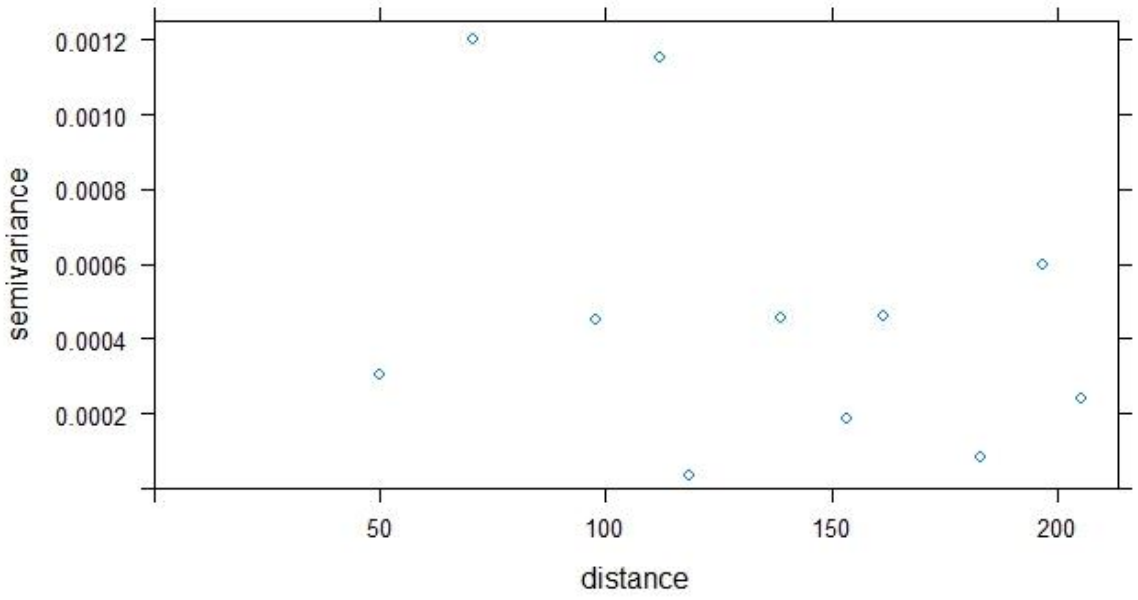

Figure C-1. Variogram of seed-rain total abundance within 15 plots of four native tree species.

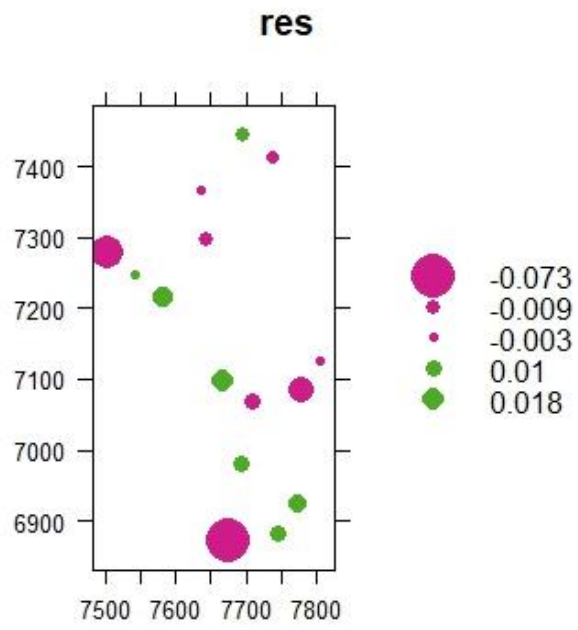

Figure C-2. Bubbleplot of total seed abundance among 15 plots of four native tree species.

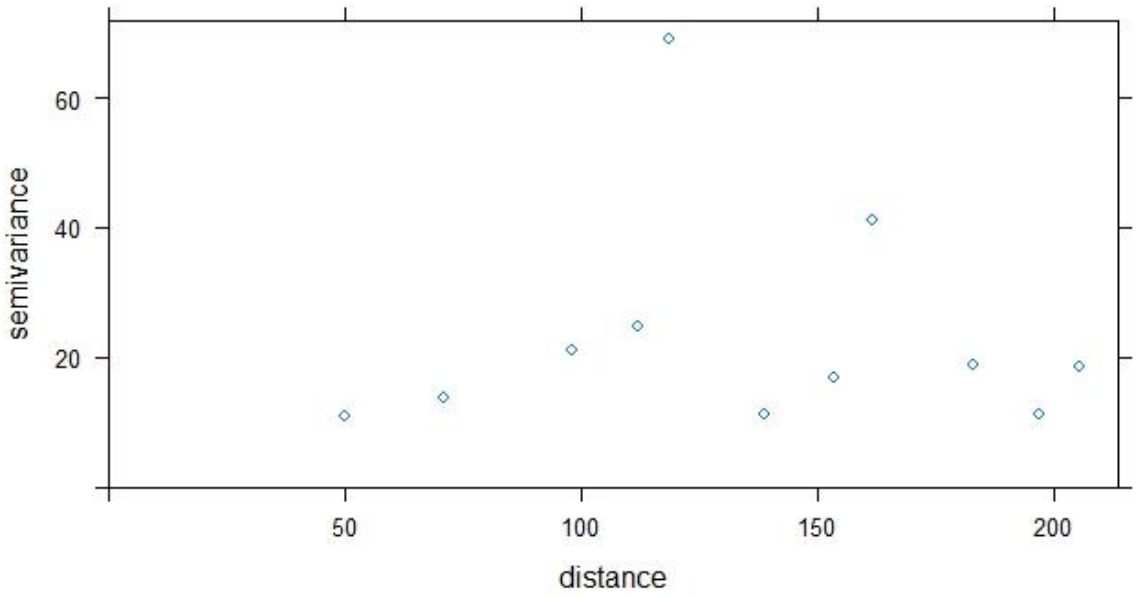

Figure C-3. Variogram of seed-rain species richness within 15 plots of four native tree species.

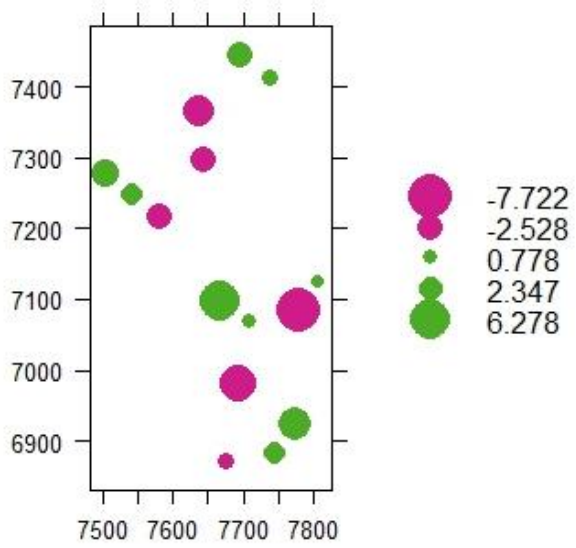

Figure C-4. Bubbleplot of species richness in seed rain among 15 plots of four native tree species.

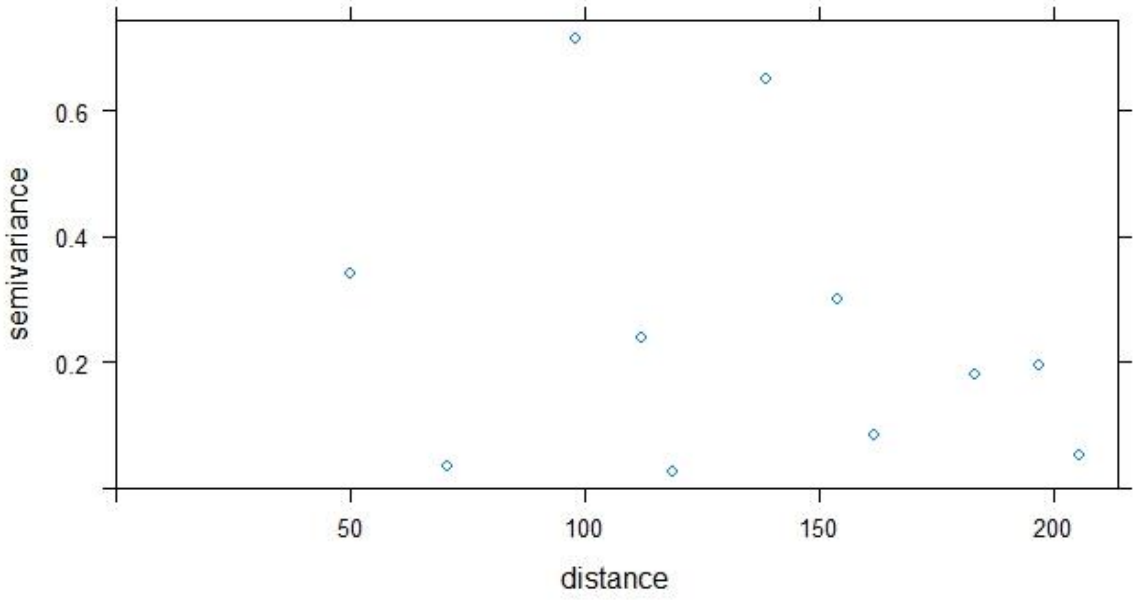

Figure C-5. Variogram of seed-rain species diversity within 15 plots of four native tree species.

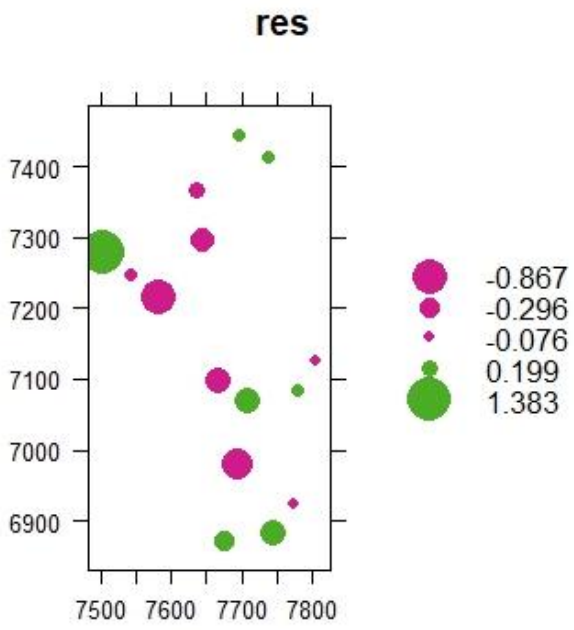

Figure C-6. Bubble plot of species diversity in seed rain among 15 plots of four native tree species.

APPENDIX D. MOST ABUNDANT SPECIES BY SEED SIZE

Table D-1. Top five most abundant small-seeded species.

				Annual Abundance				
Species	**Life form**	**Dispersal Mode**	**Successional Status**	**Hial**	**Viko**	**Pema**	**Vogu**	**Total**
Miconia affinis	Shrub	Animal	Secondary	33008	1332	1889	413	36642
Piper colonense	Shrub	Animal		5899	13986	6799	2385	29069
Miconia multispicata	Tree	Animal	Secondary	6000	11380	1518	666	19564
Alchorneopsis floribunda	Tree	Animal	Generalist	612	1697	10780	267	13356
Piper auritifolium	Shrub	Animal		0	0	11550	0	11550

Table D-2. Top five most abundant medium-seeded species.

				Annual Abundance				
Species	**Life form**	**Dispersal Mode**	**Successional Status**	**Hial**	**Viko**	**Pema**	**Vogu**	**Total**
Sabacia villosa	Liana	Animal	Generalist	1488	441	281	435	2645
Myrcia splendens	Shrub	Animal		723	4	165	17	909
Sabacia panamensis	Liana	Animal	Generalist	296	18	1	36	351
Vochysia ferruginea	Tree	Wind	Secondary	140	11	141	21	313
Guatteria recurvisepala	Tree	Animal		172	6	45	7	230

Table D-3. Top five most abundant large-seeded species.

				Seed Abundance				
Species	**Life form**	**Dispersal Mode**	**Successional Status**	**Hial**	**Viko**	**Pema**	**Vogu**	**Total**
Tetrapterys sp	Liana	Wind	Generalist	0	0	0	7	7
Vochysia guatemalensis	Tree	Wind	Secondary	1	5	0	0	6
Virola koschnyi	Tree	Animal	Generalist	1	0	1	1	3
Schlegelia fastigiata	Liana	Animal	Generalist	0	1	0	2	3
Paullinia fasciculata	Liana	Animal	Generalist	0	2	0	0	2

APPENDIX E. ANNUAL SEED RAIN ABUNDANCE ACCORDING TO MESH SIZE

Table E-1. Annual abundance of seed rain according to mesh size with species attributes.

Species	Life Form	Dispersal Mode	Seed size	Successional Affinity	Regular Mesh	Fine Mesh
Adelobotrys adscendens	Liana	Animal	Very Small	Generalist	0	139
Alchorneopsis floribunda	Tree	Animal	Small	Generalist	6245	7111
Annona papilionella	Tree	Animal	Medium	Secondary	6	15
Apeiba membranacea	Tree	Mechanical	Small	Generalist	0	7
Aristolochia sprucei	Liana	Wind	Small	Secondary	13	25
Asterogyne martiana	Palm	Animal	Medium	Old Growth	2	1
Bertiera guianensis	Shrub	Animal	Small		0	41
Bignonia binata	Liana	Wind	Medium	Generalist	1	0
Brosimum lactescens	Tree	Animal	Medium	Old Growth	1	3
Bursera simaruba	Tree	Animal	Medium		1	0
Byrsonima crassifolia	Tree	Animal	Medium	Secondary	9	0
Casearia arborea	Tree	Animal	Small	Secondary	9	48
Cecropia insignis	Tree	Animal	Small	Secondary	2	354
Cecropia obtusifolia	Tree	Animal	Small	Generalist	165	2628
Cespedesia spathulata	Tree	Wind	Small	Generalist	0	4
Cestrum schlechtendalii	Shrub	Animal	Medium		1	3
Clethra sp	Tree	Animal	Small		0	1
Clidemia crenulata	Shrub	Animal	Very Small		0	661
Clidemia densiflora	Shrub	Animal	Very Small		0	20
Clidemia dentata	Shrub	Animal	Very Small		0	192
Clidemia discolor	Shrub	Animal	Very Small		0	4
Clidemia japurensis	Shrub	Animal	Very Small		2277	571
Conostegia subcrustulata	Shrub	Animal	Small		0	1
Conostegia xalapensis	Shrub	Animal	Very Small		0	2
Cordia alliodora	Tree	Wind	Medium	Secondary	19	22
Cordia bicolor	Tree	Animal	Medium	Secondary	7	0
Davilla nitida	Liana	Animal	Small	Secondary	1	156
Dendropanax arboreus	Tree	Animal	Small	Old Growth	0	1
Doliocarpus multiflorus	Liana	Animal	Medium	Generalist	32	41
Euterpe precatoria	Palm	Animal	Medium	Old Growth	4	1

Table E-1. (continued)

Species	Life Form	Dispersal Mode	Seed size	Successional Affinity	Regular Mesh	Fine Mesh
Ficus colubrinae	Tree	Animal	Small		0	30
Ficus donnell-smithii	Shrub	Animal	Small		0	4
Ficus insipida	Tree	Animal	Small		547	592
Ficus nymphaefolia	Tree	Animal	Small		19	210
Ficus pertusa	Shrub	Animal	Small		0	5
Ficus sp	NA	Animal	Small		1	87
Ficus sp2	NA	Animal	Small		0	5
Forsteronia myriantha	Liana	Wind	Small	Generalist	0	1
Goethalsia meiantha	Tree	Wind	Small	Secondary	2	0
Gouania polygama	Liana	Wind	Small	Generalist	199	103
Guatteria aeruginosa	Tree	Animal	Medium	Old Growth	1	1
Guatteria amplifolia	Tree	Animal	Medium	Secondary	5	3
Guatteria recurvisepala	Tree	Animal	Medium		169	61
Hamelia xerocarpa	Shrub	Animal	Very Small		0	2
Hampea appendiculata	Tree	Animal	Medium	Secondary	3	3
Heisteria scandens	Liana	Animal	Medium	Old Growth	0	1
Hieronyma alchorneoides	Tree	Animal	Small	Generalist	21	40
Iriartea deltoidea	Palm	Animal	Large	Old Growth	1	0
Jacaranda copaia	Tree	Wind	Small	Secondary	1	13
Laetia procera	Tree	Animal	Small	Secondary	13	36
Lauraceae	NA	Animal	Large		0	1
Leandra granatensis	Tree	Animal	Very Small		0	1130
Leandra longicoma	Shrub	Animal	Very Small		0	9
Luehea seemannii	Tree	Wind	Small	Generalist	12	50
Mandevilla hirsuta	Liana	Wind	Medium	Generalist	9	54
Mendoncia tonduzii	Liana	Animal	Medium	Generalist	0	1
Miconia affinis	Shrub	Animal	Very Small	Secondary	2838	33804
Miconia approximata	Shrub	Animal	Very Small		0	6
Miconia elata	Tree	Animal	Small	Secondary	0	172
Miconia lacera	Shrub	Animal	Very Small		0	237
Miconia ligulata	Shrub	Animal	Very Small		0	86
Miconia multispicata	Tree	Animal	Small	Secondary	6530	13034
Miconia nervosa	Shrub	Animal	Very Small		0	1

Table E-1. (continued)

Species	Life Form	Dispersal Mode	Seed size	Successional Affinity	Regular Mesh	Fine Mesh
Miconia prasina	Shrub	Animal	Very Small		0	2
Miconia stevensiana	Tree	Animal	Very Small		0	1
Myrcia splendens	Shrub	Animal	Medium		453	456
Nectandra membranacea	Tree	Animal	Medium		3	3
Neea laetevirens	Tree	Animal	Small	Secondary	33	1
Palicourea guianensis	Shrub	Animal	Small		1	0
Paullinia fasciculata	Liana	Animal	Large	Generalist	0	2
Paullinia granatensis	Liana	Animal	Large	Old Growth	0	1
Paullinia ingifolia	Liana	Animal	Large	Old Growth	1	0
Piper aduncum	Shrub	Animal	Very Small		0	121
Piper auritifolium	Shrub	Animal	Small		11550	0
Piper auritum	Shrub	Animal	Very Small		0	325
Piper colonense	Shrub	Animal	Small		1569	27500
Piper melanocladum	Shrub	Animal	Small		0	2
Piper multiplinervium	Liana	Animal	Small	Old Growth	42	1314
Piper peltatum	Shrub	Animal	Very Small		0	65
Piper sancti-felicis	Shrub	Animal	Very Small		0	82
Piper schiedeanum	Shrub	Animal	Small		0	2
Piper sp	Shrub	Animal	Small		0	76
Piper trigonum	Shrub	Animal	Small		0	28
Piptocarpha poeppigiana	Shrub	Wind	Small		670	2922
Prestoea decurrens	Palm	Animal	Medium	Old Growth	0	1
Protium sp	Tree	Animal	Large		1	0
Psychotria brachiata	Shrub	Animal	Small		5	5
Psychotria chiapensis	Shrub	Animal	Medium		3	12
Psychotria gracilenta	Shrub	Animal	Small		12	6
Psychotria luxurians	Tree	Animal	Small		2	0
Psychotria marginata	Shrub	Animal	Small		2	8
Psychotria panamensis	Tree	Animal	Medium	Old Growth	0	3
Psychotria poeppigiana	Shrub	Animal	Medium		5	0
Psychotria sp	Shrub	Animal	Small		0	2
Rubiaceae	NA	Animal	Small		1	81
Sabicea panamensis	Liana	Animal	Medium	Generalist	0	351
Sabicea villosa	Liana	Animal	Medium	Generalist	608	2037
Schefflera nicaraguensis	Shrub	Animal	Medium		0	1

Table E-1. (continued)

Species	Life Form	Dispersal Mode	Seed size	Successional Affinity	Regular Mesh	Fine Mesh
Schlegelia fastigiata	Liana	Animal	Large	Generalist	0	3
Senna papillosa	Tree	Animal	Small		1	0
Serjania mexicana	Liana	Wind	Medium	Generalist	0	1
Serjania pyramidata	Liana	Wind	Medium	Generalist	45	33
Simarouba amara	Tree	Animal	Medium	Secondary	92	33
Siparuna grandiflora	Shrub	Animal	Small		0	1
Siparuna pauciflora	Shrub	Animal	Medium		0	1
Siparuna thecaphora	Shrub	Animal	Small		0	1
Smilax officinalis	Liana	Animal	Medium	Generalist	0	1
Solanum rugosum	Shrub	Animal	Small		0	27
Talauma gloriensis	Tree	Animal	Medium		0	2
Tetrapterys sp	Liana	Wind	Large	Generalist	0	7
Urera caracasana	Shrub	Animal	Small		0	5
Virola koschnyi	Tree	Animal	Large	Generalist	0	3
Virola sebifera	Tree	Animal	Medium	Generalist	6	13
Vismia baccifera	Tree	Animal	Small	Secondary	0	276
Vismia billbergiana	Tree	Animal	Small		279	205
Vismia macrophylla	Tree	Animal	Small		0	433
Vochysia ferruginea	Tree	Wind	Medium	Secondary	64	249
Vochysia guatemalensis	Tree	Wind	Large	Secondary	3	3
Warszewiczia coccinea	Tree	Wind	Small	Old Growth	0	23
Xylopia sericophylla	Tree	Animal	Medium	Secondary	20	144
Zanthoxylum panamense	Tree	Animal	Small	Secondary	1	9

APPENDIX F. SPECIES NOT CAPTURED IN SEED RAIN IN EACH MESH SIZE

Table F-1. Species not captured in regular (1 × 1 mm) mesh traps.

Species	Life Form	Dispersal Mode	Seed Size	Successional Status
Adelobotrys adscendens	Liana	Animal	Very Small	Generalist
Apeiba membranacea	Tree	Mechanical	Small	Generalist
Bertiera guianensis	Shrub	Animal	Small	
Cespedesia spathulata	Tree	Wind	Small	Generalist
Clethra sp	Tree	Animal	Small	
Clidemia crenulata	Shrub	Animal	Very Small	
Clidemia densiflora	Shrub	Animal	Very Small	
Clidemia dentata	Shrub	Animal	Very Small	
Clidemia discolor	Shrub	Animal	Very Small	
Conostegia subcrustulata	Shrub	Animal	Small	
Conostegia xalapensis	Shrub	Animal	Very Small	
Dendropanax arboreus	Tree	Animal	Small	Old-growth
Ficus colubrinae	Tree	Animal	Small	
Ficus donnell-smithii	Shrub	Animal	Small	
Ficus pertusa	Shrub	Animal	Small	
Ficus sp2	Unknown	Animal	Small	
Forsteronia myriantha	Liana	Wind	Small	Generalist
Hamelia xerocarpa	Shrub	Animal	Very Small	
Heisteria scandens	Liana	Animal	medium	Old-growth
Lauraceae	Unknown	Animal	Large	
Leandra granatensis	Tree	Animal	Very Small	
Leandra longicoma	Shrub	Animal	Very Small	
Mendoncia tonduzii	Liana	Animal	medium	Generalist
Miconia approximata	Shrub	Animal	Very Small	
Miconia elata	Tree	Animal	Small	Secondary
Miconia lacera	Shrub	Animal	Very Small	
Miconia ligulata	Shrub	Animal	Very Small	
Miconia nervosa	Shrub	Animal	Very Small	
Miconia prasina	Shrub	Animal	Very Small	
Miconia stevensiana	Tree	Animal	Very Small	

Table F-1. (continued)

Species	Life Form	Dispersal Mode	Seed Size	Successional Status
Paullinia fasciculata	Liana	Animal	Large	Generalist
Paullinia granatensis	Liana	Animal	Large	Old-growth
Piper aduncum	Shrub	Animal	Very Small	
Piper auritum	Shrub	Animal	Very Small	
Piper melanocladum	Shrub	Animal	Small	
Piper peltatum	Shrub	Animal	Very Small	
Piper sancti-felicis	Shrub	Animal	Very Small	
Piper schiedeanum	Shrub	Animal	Small	
Piper sp	Shrub	Animal	Small	
Piper trigonum	Shrub	Animal	Small	
Prestoea decurrens	Palm	Animal	medium	Old-growth
Psychotria panamensis	Tree	Animal	medium	Old-growth
Psychotria sp	Shrub	Animal	Small	
Sabicea panamensis	Liana	Animal	medium	Generalist
Schefflera nicaraguensis	Shrub	Animal	medium	
Schlegelia fastigiata	Liana	Animal	Large	Generalist
Serjania mexicana	Liana	Wind	medium	Generalist
Siparuna grandiflora	Shrub	Animal	Small	
Siparuna pauciflora	Shrub	Animal	medium	
Siparuna thecaphora	Shrub	Animal	Small	
Smilax officinalis	Liana	Animal	medium	Generalist
Solanum rugosum	Shrub	Animal	Small	
Talauma gloriensis	Tree	Animal	medium	
Tetrapterys sp	Liana	Wind	Large	Generalist
Urera caracasana	Shrub	Animal	Small	
Virola koschnyi	Tree	Animal	Large	Generalist
Vismia baccifera	Tree	Animal	Small	Secondary
Vismia macrophylla	Tree	Animal	Small	
Warszewiczia coccinea	Tree	Wind	Small	Old-growth

Table F-2. Species not captured in fine-mesh traps.

Species	Life Form	Dispersal Mode	Seed Size	Successional Status
Bignonia binata	Liana	Wind	Medium	Generalist
Bursera simaruba	Tree	Animal	Medium	
Byrsonima crassifolia	Tree	Animal	Medium	Secondary
Cordia bicolor	Tree	Animal	Medium	Secondary
Goethalsia meiantha	Tree	Wind	Small	Secondary
Iriartea deltoidea	Palm	Animal	Large	Old growth
Palicourea guianensis	Shrub	Animal	Small	
Paullinia ingifolia	Liana	Animal	Large	Secondary
Piper auritifolium	Shrub	Animal	Small	
Protium sp	Tree	Animal	Large	
Psychotria luxurians	Tree	Animal	Small	
Psychotria poeppigiana	Shrub	Animal	Medium	
Senna papillosa	Tree	Animal	Small	

APPENDIX G. ECOLOGICAL TRAITS OF VERY-SMALL SEEDED SPECIES IN SEED RAIN

Table G-1. Ecological traits and abundance of species with seed size ≤ 1 mm in two mesh sizes.

Species	Life Form	Dispersal Mode	Successional Status	Regular Mesh	Fine Mesh
Adelobotrys adscendens	Liana	Animal	Generalist	0	139
Clidemia crenulata	Shrub	Animal		0	661
Clidemia densiflora	Shrub	Animal		0	20
Clidemia dentata	Shrub	Animal		0	192
Clidemia discolor	Shrub	Animal		0	4
Clidemia japurensis	Shrub	Animal		2277	571
Conostegia xalapensis	Shrub	Animal		0	2
Hamelia xerocarpa	Shrub	Animal		0	2
Leandra granatensis	Tree	Animal		0	1130
Leandra longicoma	Shrub	Animal		0	9
Miconia affinis	Shrub	Animal	Secondary	2838	33804
Miconia approximata	Shrub	Animal		0	6
Miconia lacera	Shrub	Animal		0	237
Miconia ligulata	Shrub	Animal		0	86
Miconia nervosa	Shrub	Animal		0	1
Miconia prasina	Shrub	Animal		0	2
Miconia stevensiana	Tree	Animal		0	1
Piper aduncum	Shrub	Animal		0	121
Piper auritum	Shrub	Animal		0	325
Piper peltatum	Shrub	Animal		0	65
Piper sancti-felicis	Shrub	Animal		0	82

APPENDIX H. INTERACTION BETWEEN MESH SIZE AND OVERSTORY TREE SPECIES

Table H-1. ANOVAs for the interaction between mesh size and overstory tree species.

Response	Interaction	df	F-value	P-value
Abundance	*Mesh* × *tree species*	3	1.73	0.17
Species Richness	*Mesh* × *tree species*	3	7.71	0.0002
Shannon-Weiner Diversity	*Mesh* × *tree species*	3	0.58	0.63
Pielou's Evenness	*Mesh* × *tree species*	3	0.20	0.89

Table H-2. Species richness one-way ANOVAs of interaction between mesh size and overstory tree species.

Overstory Tree Species	df	t ratio	P-value
Hieronyma	56	11.5	< 0.0001
Virola	56	14.0	< 0.0001
Pentaclethra	56	7.3	< 0.0001
Vochysia	56	10.5	< 0.0001